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UNIVERSITY OF ALBERTA

RUMINO-RETICULAR FUNCTION IN CATTLE: MOTILITY, KINETICS AND DIGESTION

BY

©

ERASMUS N. K. OKINE

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
IN
ANIMAL NUTRITION

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA
FALL 1990

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THE UNDERSIGNED CERTIFY THAT THEY HAVE READ, AND RECOMMENDED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH FOR ACCEPTANCE, A THESIS ENTITLED RUMINO-RETICULAR FUNCTION IN CATTLE: MOTILITY, KINETICS AND DIGESTION.

SUBMITTED BY ERASMUS N. K. OKINE IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ANIMAL NUTRITION.

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ABSTRACT

A series of four studies was conducted: (1), to examine various aspects of rumino-reticular function and how these functions relate to passage rates of digesta from the rumino-reticulum (RR) and (2) to examine how passage rate of digesta could be changed and the mechanisms by which passage rates were changed with the view of finding ways of manipulating RR function.

In study 1, the relationships between RR fluid and particulate passage rates and foam production in RR contents were examined. Rumen-fluid dilution rates (FDR) 0-2 h and 2-7 h after provision of feed were higher ($P<.05$) for bloat-resistant (group A) (0.205 and 0.16/h) than for bloat-susceptible (group B) cattle (0.093 and 0.086/h). Heights of foam produced from samples of RR fluid in cylinders after provision of feed were higher ($P<.05$) in group B than in group A cattle (150 and 240 mm at 2 h and 60 and 150 mm at 4 h, respectively). Foam heights recorded 2 and 4 h after feeding were negatively correlated ($r = -0.74$ and -0.85 respectively; $P<.05$) with FDR of RR fluid. Low FDR in group B cattle and the consequent high foam production during and after feeding were identified as the major factors responsible for increased tendency for animals to bloat.

Addition of 24 kg weights to the rumen of cattle at a constant feed intake caused a 29% decrease in methane production associated with increases of 39 and 30% in passage rates constants for particulate matter and rumen fluid in study 2. Frequency of reticular contraction was not significantly ($P = 0.76$) related with variation

in passage of digesta from the RR whereas duration (P = 0.0001), amplitude (P = 0.0001) and the index of work done per contraction (amplitude x duration) (P = 0.0001) were. Heat production of steers was not influenced by extra weight in the RR. The proportion of large particles in the feces was significantly correlated (P = 0.90) with duration of reticular contractions (study 3). Four cows were fed at different feeding levels in study 4. At maintenance (M) and 1.7M feeding levels, 1.7 and 2.3 g of neutral detergent fiber (NDF) were transferred from the RR per reticular contraction. Amounts of NDF transferred per second the reticulum was contracted were 0.33 and 0.30 g at M and 1.7M respectively. Corresponding amounts were 0.25 and 0.24 g per mm of Hg of pressure increase during a contraction of the reticulum.

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I. GENERAL INTRODUCTION

The voluntary feed intake of ruminants is thought to be limited by rumen fill, particularly when low quality forages are fed (Balch and Campling, 1962). Fermentation of dietary components, comminution and passage from the rumino-reticulum (RR) provide the means of reducing rumen fill (Mertens and Ely, 1982; Ulyatt et al., 1986). It has been well established that the passage of undegraded feed residues from the RR is essential for further intake to occur (Dixon et al., 1983), and that rate of passage may be the major factor controlling forage intake and digestibility of diets in cattle and sheep (Colucci et al., 1982; Van Soest, 1982; Welch, 1986). Passage rate of digesta from the RR therefore is an important aspect of ruminant nutrition.

Passage from the RR is influenced by ruminoreticular contractions. It has been generally believed that there is a positive relationship between frequency of ruminoreticular contractions and passage rate from the RR (Reid, 1963; Sissons et al., 1984), but this concept is based on limited data. Indeed, substantial progress has been made in the last decades in understanding the organization of myogenic control systems, the presence of various types of intrinsic and extrinsic nerves innervating the RR, and the presence of neurotransmitters and neuromodulators involved in the motor activity and secretory function of the ruminant stomach. However, very little progress has been made in understanding the relationship between motor activity and passage from the RR (Weyns et al., 1987).

Since the rate of passage of digesta from the RR is so important in terms of the effect it has on voluntary intake and the overall productivity of the animal, any improvements in our knowledge of the factors controlling passage and RR function will ultimately lead to improvements in the efficiency of animal production. A series of studies was therefore undertaken on various aspects of ruminoreticular function and how those functions related to passage rates. In study 1, the relationships between rumen fluid and particulate passage rates and foam production in rumen contents (an index of bloat potential) were examined. Study 2 examined how passage rate of digesta could be changed and the mechanism by which passage rate was changed, with the primary aim of finding ways of manipulating rumen function. Study 3 involved measurements of the physical changes in the distribution of fecal particles in an in-depth examination of the consequences of changing passage rates. Finally, in study 4, the effects of feed intake on fractional passage rate and the relationships between reticular motility attributes and both total outflow and fractional passage rate from the rumino-reticulum were evaluated.

1.1 Rate of passage

1.1.1 Importance

The productivity of the ruminant animal is dependent on the voluntary intake and the extent to which the feed is digested in the RR (Faichney, 1986). Clearance of feed residues from the RR has long been established as a major process determining, and therefore controlling, both intake and digestion of forages (Grovum and Williams, 1973; Faichney and Griffiths, 1978). Clearance of residues from the RR has been reported to be limited by two main processes: physical reduction in particle size by comminution plus microbial digestion and physical passage from the RR (Poppi et al., 1980; Ulyatt et al., 1986). The passage of contents from the RR is controlled by both the volume and fractional passage rate (FPR), where FPR is the constant fraction of digesta which leaves the RR pool per unit time. If increased RR clearance rates are achieved by increased FPR, there is a reduction in the time available for the processes of fermentation, microbial protein synthesis and absorption to occur in the RR and thus the extent of digestion may be reduced (Dixon et al., 1983). It is therefore accepted that retention time and digestibility are positively correlated (Warner, 1981) while passage and digestibility are negatively correlated (Colucci et al., 1982).

1.1.2 Fluid passage rate

Generally as dry matter intake increases, ruminal fluid volume, dry matter percentage in ruminal digesta and fractional particulate and fluid dilution rates (FDR) all increase. The effect of increased intake on FDR is, however, greater than the effect on fractional particulate passage rate (Owens and Goetsch, 1986). Evans (1981) reported that FDR increases with feed intake because water intake usually parallels dry matter intake. Garza and Owens (1989) also reported high water intake with increase in dry matter intake and that, of drinking water consumed, about 71% never mixes with ruminal contents. However, infusion of water into the rumen did not increase ruminoreticular fluid dilution rate although infusion of solutions with high osmotic pressures increased fluid dilution rates (Harrison et al., 1975). Solutes derived from feed, saliva, or products of fermentation should therefore influence fluid passage rates (Owens and Goetsch, 1986). Feed composition and processing also influence fluid dilution rate since they influence mastication and rumination and hence salivary flow (Owens and Goetsch, 1986). Fluid dilution rate is greater for diets with a higher proportion of roughages as opposed to concentrate diets (Warner, 1981). Supposedly this is due to increased mastication and salivation and increased stimulation of the propulsive activity of the RR (Warner, 1981).

1.1.3 Particulate passage rates

1.1.3.1 Factors affecting particulate passage rates

Increases in feed intake usually result in higher fractional passage rates and outflows of both particulate matter and fluid from the RR and through the total gastrointestinal tract (Faichney, 1986). The converse is also generally true; a decreased level of intake is associated with a decreased fractional passage rate and outflow of particulate matter (Evans, 1981). However this relationship may not always hold. Robinson et al. (1987), reported that based on rumen evacuation, fractional passage rate declined linearly as intake decreased but, based on chromium-mordanted fiber, fractional passage rate showed a quadratic response, being at a maximum at intermediate levels of intake. Ulyatt et al. (1984) and von Keyserlingk and Mathison (1989) have also reported a lack of influence of feed intake on fractional passage rate while total outflow increased.

While the effect of feed intake on fractional passage rates remains equivocal, the inextricable link between intake of roughages and the total outflow rate of digesta through the RR has led to the supposition that treatments which facilitate the production of small particles in the RR and their outflow should increase the outflow rate and the ad libitum intake of feedstuff. However the effect of grinding of roughages on passage rate is not well established. Although results of Thomson and Beever (1980) and of Warner (1981) suggest that grinding and pelleting result in increased rates of passage and shorter mean retention times, Campling and Freer (1962) reported little difference in mean retention times in the alimentary tracts of dairy cows fed to appetite. Alternatively, they found differences in mean retention times with grinding when animals were fed at restricted intakes. Weston (1989) suggests that the equivocal effect of grinding on passage rates may be the consequence of the opposing effects of grinding on two determinants of clearance rates. On one hand, grinding reduces digesta flow rate thereby tending to decrease clearance rate (Weston, 1974) while on the other hand grinding increases particle concentration in the reticulum which tends to increase clearance rates (Weston, 1989). The consequences of grinding on clearance rate therefore depends on the extent to which flow is reduced and concentration is increased (Weston, 1989).

1.1.3.2 Functional specific gravity

Density of particles has been concluded to be the sole determinant of the direction and movement of particles within the RR and a very important factor affecting the magnitude of sedimentation and/or floatation velocities and therefore of passage through the reticulo-omasal orifice (Sutherland, 1988). The importance of specific gravity has been echoed by various researchers who have reported that specific gravity affects passage of inert particles (King and Moore, 1957; Evans et al., 1973; desBordes and Welch, 1984) and chromium mordanted to the neutral detergent fiber of alfalfa (Ehle, 1984) from the rumen. desBordes and Welch (1984) reported that particles with specific gravity between 1.17 and 1.42 sank through the fibrous mat in the rumen and thus were more likely to be passed out from the rumen than were particles outside this range. Campling and Freer (1962) also concluded that with roughage diets, particles with a specific gravity of 1.12 had a shorter retention time in the total gastrointestinal tract than particles of smaller or greater specific gravity within the range 1.02 - 1.40. Thus specific gravity of particles, through its effect on passage rate, is likely to influence voluntary intake in forage-fed ruminants.

Sutherland (1988), while agreeing with the importance of specific gravity on passage rates and therefore of voluntary intake, criticized the methodology of determination of specific gravity by Campling and Freer, (1962) and Ehle, (1984). The density of digesta particles depends on the relative volumes of the particle occupied by solid components, liquid and gas. It is likely that volumes of the particle occupied by gas and liquid change quite rapidly and thus will be influenced by the conditions in which the particles were placed in the laboratory for density determinations. This makes the estimation of the in vivo density of particles prone to error (Sutherland, 1988). Using simple observations of the ratios of wet weight to dry weight of particles in which gas production had ceased and the gas space had been replaced by liquid, Sutherland (1988) obtained information on maximum densities and gas volumes and confirmed results obtained by Evans et al. (1973) of a negative relationship between particle size and specific gravity. Hooper and Welch (1985) also confirmed this relationship and showed that the rate of change in functional gravity of particles with time was also dependent on particle size.

The initial idea of the relationship between particle size and volume are contained in the "hotel theory" of Van Soest (1975). He postulated that as particles become smaller, the ratio of enclosed "room" volume to structural wall decreases and the maximum density increases. Thus, as particles become smaller they tend to have higher intrinsic maximum densities, and therefore would need greater proportions of their fluid volumes to be filled with gas to achieve buoyancy. The particles however have a poor architecture for gas entrapment and an increased ratio of surface area to volume that would facilitate gas loss (Sutherland, 1988). As a consequence the effective specific gravity within the RR is closely determined by particle size, which therefore becomes the major determinant of passage rate.

1.1.3.3 Critical size theory

In practice, although the RR of both sheep and cattle contain large proportions of long fibrous materials, the digestive organs beyond the omasum contain few particles of more than 1 or 2 mm in length for sheep and cattle, respectively, (Pearce, 1967; Reid et al., 1977; Poppi et al., 1980; Ulyatt et al., 1986). Balch (1950) was among the first to report that few large particles exit the rumen. Similar results were obtained by Poppi et al., (1980) who then proposed a threshold size above which little or no particles exited the rumen. Faichney (1986) argued that the threshold for particle size passing the reticulo-omasal orifice is a constant not influenced by feed preparation and that changes in fecal particle size relate only to changes in the distribution of particles in the RR already within the size range having a probability of removal from the RR. In contrast Van Soest, (1982), Smith et al., (1983) and Van Soest et. al. (1988) argued that the limit in particle size that can exit the rumen is influenced by the dietary distribution in particle size and that level of intake and the type of feed has an effect on the size of fecal particles.

Comminution of feed particles largely occurs by chewing during eating and rumination with microbial activity contributing to weaken the internal structure of the plant cell wall (Faichney, 1986; Ulyatt et al., 1986). Chewing during eating generally reduces a maximum of 15% of forage dry matter to below the critical size that can escape through the reticulo-omasal orifice, irrespective of feed type, whereas chewing during rumination reduces a maximum of 16% of fresh forage and 39% of hay, dietary dry matter regurgitated to this size (Ulyatt et al., 1986). When refractory material is considered chewing during rumination, with 33-51% efficiency in large particle reduction appears to be more important than chewing during eating with an efficiency of 9-23% in reducing large particles to sizes less than the critical size (Chai et al., 1988).

1.1.3.4 Probabilities of escape

Particles leave the RR in aqueous suspension. If the particles were evenly distributed within the RR and there was no constraint exerted at the reticulo-omasal orifice, particles would be expected to have the same fractional outflow rates from the RR as the liquid phase markers (Sutherland, 1988). However, it is recognized that the probability of escape from the RR is inversely related to particle size (Balch, 1950; Poppi et al., 1980; Weston and Cantle, 1984; Weston, 1988) and that even the finest particles flow from the rumen more slowly than fluid (Faichney, 1986). The decreased probability of escape that exists for particles of larger sizes has been attributed to several processes acting either individually or in conjunction with each other. These processes include sequestration in the dorsal raft, filtering effects in the passage of particles through the raft to the ventral sac enroute to the reticulum, discriminatory sieving effects within the reticulum itself or at the reticulo-omasal orifice, and entrapment of large particles within the leaves of the omasum and susequent back-flow to the RR (Sutherland, 1988). It is generally accepted that discrimination against the passage of large particles occurs before the omasum (Balch and Campling, 1962; Uden and Van Soest, 1982; Waghorn et al., 1986; Weston, 1989). Particulate matter that is presented to the reticulo-omasal orifice is from the ventral layer and that material from the dorsal area of the rumen must pass through the underlying layer to exit the RR (Sutherland, 1988). Particle distribution within the dorsal rumen is generally biased toward larger particles relative to the distribution in the ventral site of the rumen of cows (Evans et al., 1973;) and in sheep (Ulyatt et al., 1984; Waghorn et al., 1986). Comparing the relative concentrations of particles of various sizes in the dorsal and ventral regions of the rumen, Sutherland (1988) reported that the concentration in the dorsal sac, was for all particle sizes, higher than that in the ventral sac. Using the ratio of the concentration of a particular particle size in the dorsal sac to that in the ventral sac which he defined as "distribution coefficient" Sutherland (1988) clearly established a negative relationship between the probability of particles exiting the rumen and their distribution coefficients; the higher the distribution coefficient, the lower the probability of escape from the rumen. A similar distribution of particles exists between the rumen and the reticulum. Weston and Cantle (1984) reported that the concentration of smaller particles in the reticulum was higher than the concentration of particles of similar size in the rumen, with a subsequent greater clearance rate from the reticulum when compared with the rumen. McBride et al. (1984), reported that the reticulo-omasal orifice does not constitute a barrier to the passage of large particles and gives credence to the conventional wisdom that the low probability of escape of large particles is due to their failure to navigate through the raft. However, Weston and Cantle (1984), reported the differential passage of particles through the omasum, with larger particles having lower fractional clearance rates with a possibility that the back-flow from the omasum to the reticulum is enriched with larger particles.

1.1.3.5 Rumino-reticular motility attributes

1.1.3.5.1 Motility patterns

The gross movements of the ruminant forestomach are variously termed "primary and secondary cycle movements", "A and B" sequences and "mixing and eructation contractions" (Wyburn, 1980). The primary cycle which promotes mixing, fermentation, absorption, particle breakdown, and onward passage of digesta from the RR starts with two separate reticular contractions in cattle (Grovum, 1986). This is followed by sequential contractions of the cranial, dorsal and ventral sacs and finally of the ventral blind sac. The primary cycle occurs, on the average of approximately one minute while the secondary cycle occurs, on average after every second primary cycle and is comprised of sequential contractions of the various sacs in the RR starting with contraction of the ventral blind sac (Leek, 1987). The secondary cycle movements are particularly responsible for the eructation of ruminal fermentation gases (Leek, 1987).

1.1.3.5.2 Synchronization with reticulo-omasal orifice and omasal activity

Some of the attributes of RR motor activity that determine passage of digesta include frequency of contraction, amplitude and duration of contractions, whether the contractions propagate or not and, if so, in which direction the propagation occurs (Sarna, 1985). Although the contribution of the individual attributes of RR motor activity in influencing passage from the RR appear simple, their combined effects have been difficult to evaluate since these attributes defy visual analysis and may vary from one contraction to another, even in an organ like the RR where contractions are fairly regular and uniform (Grovum, 1986).

In smaller ruminants like the sheep and goat, passage of digesta from the RR is achieved by synchronization of the contraction of the reticulum with the opening of the reticulo-omasal orifice and the motility of the omasum which acts as an aspiration pump (Deswysen, 1987). In cattle, the motility of the reticulum is apparently not synchronized with that of the omasum, and the omasum, due to its rather large size (28% vs 5% of the total forestomach volume in cattle and sheep, respectively), does not act as an aspiration pump (Deswysen, 1987). Passage of digesta from the RR in cattle is therefore achieved by synchronization of the contraction of the reticulum with the opening of the reticulo-omasal orifice. In addition, there is 50% more pressure in the rumino-reticulum compared to the abomasum at the end of the second phasic contraction of the reticulum when the orifice is opened (Deswysen, 1987).

1.1.3.5.3 Effect of feeding on motility

The degree of RR motility is a major factor in the digestion, synthesis and absorption of nutrients from the RR (Mooney et al., 1971). Diet is thought to affect RR motility through palatability, the associated act of feeding and tactile stimulation, and stretch of the wall of the RR, all of which affect frequency of contractions (Reid, 1963). Reid (1963) reported that in sheep the extent and persistence of the increases of strength and frequency of rumen contractions during feeding appeared to be primarily determined by dietary factors. The reported changes were most complete and most persistent when coarse hay was fed. In contrast, the changes in strength and frequency were least complete and least persistent when the feed was a pelleted meal (Reid, 1963). Colvin et al., (1978) working with cattle found that, when fresh alfalfa tops were fed, the frequency of the reticular contractions was higher, but the amplitude of contraction was smaller, than when cattle were fed oat hay. Lirette et al., (1988) observed no consistent diet effect on contractile frequency of the reticulum of steers at the maintenance feeding level when brome and alfalfa hays, alfalfa silage and barley concentrate were compared.

Generally, frequency of reticular contraction increases during feeding, but not during rumination or resting (Grovum, 1986). Osuji et al., (1975) reported that when sheep were fed dried grass pellets, the frequency of reticular contractions was greater during eating but not during resting or ruminating, than when sheep were fed chopped fresh or dried grass. Similar results of increases in frequency of reticular contractions were obtained in sheep fed alfalfa pellets in comparison with sheep fed alfalfa chaff or grass (Waghorn and Reid, 1977). Addition of roughage to concentrate diets increases the frequency of reticular contraction. This increase has been interpreted to be due to a moderate distension of the RR, a relatively higher pH, and a lower concentration of volatile fatty acids (Grovum, 1984). Distension of the RR wall also appears to influence the amplitude of reticular contractions. Amplitude of contractions was suppressed when diets of milk were fed in comparison with contractions in roughage-fed calves (McGilliard et al., 1965).

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II. RELATIONS BETWEEN PASSAGE RATES OF RUMEN FLUID AND PARTICULATE MATTER AND FOAM PRODUCTION IN RUMEN CONTENTS OF CATTLE FED DIFFERENT DIETS *AD LIB*[1]

2.1 INTRODUCTION

Feedlot and legume bloat have both been postulated to be caused by complex interrelationships between plant, animal, environmental, and microbial factors (Mendel and Boda, 1961; Howarth et al. 1986). Among the numerous animal factors, bloat-prone cattle in comparison to non-bloating cattle have been reported to secrete less saliva during feeding and resting (Mendel and Boda, 1961), have a higher particulate matter content in the rumen as estimated by chlorophyll content (Majak et al. 1983, 1986a; Howarth et al. 1986), and also have larger rumen volumes (Cockrem et al. 1983).

Indeed the evidence of a higher chlorophyll concentration in digesta contents in spite of larger volume of rumen digesta in bloat-prone cattle compared with non-bloating cattle is consistent with a slower overall rate of dilution of liquid markers from the rumen of the susceptible cattle (Majak et al. 1986b). However, differences in overall rate of dilution may be inadequate to explain differences between bloat susceptible and non-susceptible animals. Although both types of cattle show increases in rumen particulate matter, as indicated by chlorophyll concentration 2 h after feeding, chlorophyll concentration in bloat-prone cattle continues to increase until 4 h after feeding while the concentration remains approximately the same as at 2 h in non-bloating cattle (Majak et al. 1983). This would indicate differential passage rates from the rumen for the bloat-types of cattle at different times after feeding or differential rates of digestion.

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[1] A version of this chapter has been published. Okine, E.K., G.W. Mathison and R.T. Hardin. 1989. Br. J. Nutr. 66:387-395.

The present study was designed to obtain information on the relationships between particulate-matter (rumen-particle) and rumen-fluid passage rates (PPR and FPR respectively) and foam production between two different groups of cattle in situations reflecting normal ingestive behaviour. It was also designed to examine the effects of changes in marker dilution curves before, during, and after feeding on the amounts of foam produced from rumen contents of cattle given various feeds.

2.2 MATERIALS AND METHODS

2.2.1 Animals and feed

Three cattle (539 kg) of Hereford breeding with a history of not being susceptible to bloat (group A), and which had been cannulated 2 years previously, and three cattle (386 kg) also of Hereford breeding with a history of being bloat-susceptible (group B) and which had been ruminally cannulated for 3 months were used in this study. Each of the three group-A cattle were randomly paired with the group-B cattle, forming three pairs of animals. These pairs were used in a split-plot experiment with whole plots being a 3 x 3 Latin Square with three periods, three diets and three animal pairs. The split-plots of the experiment were the two animal groups. Each period consisted of 30 d with one animal from each group receiving one of the three different diets.

The three diets used in the experiment were lucerne (Medicago sativa) pellets (pellets) which contained (%): 3.02 nitrogen and 45.0 cell-wall contents (CWC) on a dry matter (DM) basis, chopped lucerne hay (hay) which contained 2.21 N and 50.5 CWC, and 90.0 rolled barley grain (2.0 N and 17.2 CWC) and 10.0 chopped hay fed as a mixture (concentrate).

2.2.2 Voluntary feed intake measurements

The diets were offered ad lib. twice daily at 09.00 hours and at 16.00 hours. The first allocation of feed was about 75 % of the total with the remainder being offered at 16.00 hours. Trace mineralized salt blocks and water were available ad lib. Voluntary feed consumption was measured over 12 d by offering the diets in sufficient amounts to allow for 10 % rejection. Thereafter the feed was offered at the maximum eaten by day 12 for another 9 d before measurements commenced. On two separate occasions during each period measurements were recorded of the initial intake of individual cattle, after provision of fresh feed, until the cattle first left the feedbunk. In addition, the number of visitations made by the animals to feed was recorded and this was used to calculate the average meal size over an 8-12 h period.

2.2.3 Foam measurements

The foaming properties of rumen fluid from the various cattle were examined according to the procedure of Pressey et al. (1963). Briefly, 50 ml fresh rumen fluid were poured into a glass cylinder (20 mm i.d. and 50 mm in length) and carbon dioxide gas was bubbled through a bottom inlet at 2 KPa for 2 min, resulting in conversion of most of the fluid to foam. Foam height, measured as the height of foam at the interface of fluid and foam in the cylinder, was used as a measure of foam production. Foam instability was calculated as the difference between initial foam height and the foam height 5 min after cessation of gassing, expressed as a percentage of initial foam height.

2.2.4 Passage rate studies

FPR was determined using crystalline Co-EDTA prepared according to the procedures of Uden et al. (1980). The particulate marker used in the present study for PPR was chromium mordanted to fibre. The fibres for mordanting were prepared by soaking about 2 kg ground lucerne in water overnight. The material was then fractionated using a wet sieving procedure. The particles retained on the 1 mm screen after passing through the 2 mm were mordanted with Cr according to the method of Uden et al. (1980). The particles contained about 32 mg Cr/kg after this procedure.

FPR studies were conducted on days 22 and 30 of each period, whereas PPR was determined from Cr-mordanted particles introduced on day 22. The animals were dosed intraruminally with 5 g of cobalt and 50 g Cr-mordanted particles simultaneously at 06.00 hours on the day of passage rate studies, 3 h before feeding. In this procedure approximately half the rumen contents were removed, mixed with Co and Cr-mordanted particles, and returned to the rumen.

Rumen fluid samples for FPR were taken from various sections of the rumen at 0.5, 1, 2, 3 h after dosing with markers 3-0 h before provision of feed, then every 0.5 h for the next 2 h, and then hourly from 2 to 7 h after feed was offered. The contents were squeezed through four layers of cheesecloth, the filtrate was frozen, and the solid particles returned to the rumen. Rumen samples for PPR determination were collected at 4, 24, 48, and 72 h after administration of the mordanted particles, subsampled, and frozen for subsequent analysis.

2.2.5 Laboratory procedures

The DM of feed and rumen digesta were determined by oven drying at 80° to constant weight. N concentration of feed was determined by standard procedures (Association of Official Analytical Chemists, (AOAC), 1980), using method 2.057. Cell-wall contents were determined by the method of Goering and van Soest (1970).

A subsample of the rumen fluid (15 ml) was thawed, centrifuged (39000 g for 10 min) and the Co concentration determined after 1:5 dilution with 0.1 M-hydrochloric acid by atomic absorption spectrophotometry (AAS) (model 4000; Perkin Elmer Corp., Norwalk, Conn. 06856, USA). Cr in rumen samples was determined according to the procedure of P.H. Robinson (personal communication) after oven drying 50 g of the rumen digesta for 3 d at 60° and grinding the material to pass a 1 mm screen. The ground material (500 mg) was soaked in 60 ml of 4 M-nitric acid for 4 h at room temperature and then for 12 h at 75°. The resultant solution was centrifuged (39000 g for 5 min) with the supernatant fraction being analyzed for Cr using the AAS.

2.2.6 Calculations and statistical analysis

Movement of digesta from the rumen was calculated with reference to the CoEDTA and Cr-mordanted particle concentrations in the digesta. No correction was made for absorption of Co across the rumen wall, since no significant amounts of Co were detected in the urine.

The passage rate constants for each marker were calculated as first-order rate constants since first order kinetic equations described more than 90 % of the variance in the decline in concentration of each marker with time in thirty-three out of the thirty-six situations. Separate regressions were employed to determine the fluid dilution rates (FDR) during each sampling phase: 2.5-0 h before feeding, 0-2 h after provision of feed and 2-7 h after feed was offered. Initial rumen volumes were calculated from the weights of CoEDTA given and the concentration of the marker at zero time as estimated by extrapolation using regression points before feeding (Stokes et al. 1985).

The rate constants of both markers, foam heights, foam instabilities and rumen volumes were analyzed as a split-plot with the whole plots being a 3 x 3 Latin Square with three periods, three diets and three animal pairs. The two animal groups were the split-plot.

Rumen-fluid FDR 2.5-0 h before feeding, and 0-2 h and 2-7 h after provision of feed were regressed against foam height and foam instabilities for these times. Differences between means were determined using analyses of variance procedures. When significant diet effects were detected, the diet means were compared using the Student-Newman-Keuls' range statistic (Steel and Torrie, 1980).

2.3 RESULTS

2.3.1 Voluntary feed intake measurements

DM intakes by cattle in group A for all the diets were greater (P<.05) than intakes by cattle in group B, although the differences lacked significance when expressed relative to body-weight (Table 2.1). Also, although both mean initial intakes and average size of meal were greater (P<.05) for groups A than B, there were no differences (P>.05) when both were expressed relative to body-weight (Table 2.1).

2.3.2 Passage rate studies

Multiple-component marker concentration curves were obtained when the liquid marker was introduced 3 h before feeding (Figure 2.1 as a representative example), with a sharp decline in Co concentration tending to occur during feeding.

Before feeding no differences were seen in FDR between animal group or between diets. However, the FDR 0-2 h and 2-7 h after provision of feed were higher (P<.05) for group A than for group B (Table 2.2).

Rumen-fluid FDR 2-7 h after feed was offered were not different (P>.05) between animals given the hay and pellet diets with both diets resulting in a higher (P<.05) FDR than the concentrate diet.

Mean reticulo-rumen volumes (litres or litres /kg body-weight) were higher (P<.05) in group B cattle than in group A (Table 2.2). Diet had no influence (P>.05) on rumen volumes.

The passage rate constants of the 1-2 mm Cr-mordanted particles were greater (P<.05) for cattle fed on the concentrate diet compared with those in cattle given either hay or pellets (Table 2.2). Cr-mordanted PPR constants were not significantly influenced by cattle group type.

2.3.3 Foam measurements

Amount of foam produced from rumen fluid 3 h before feeding was not different (P>.05) between the animal groups (Table 2.3), however, the mean foam heights after provision of feed were higher (P<.05) in group B than in group A (150 and 240 mm at 2 h and 60 and 150 mm at 4 h respectively). The foam heights recorded 2 and 4 h after feeding for all diets were negatively correlated (r -0.74 and -0.85 respectively; P<.05) (Table 2.4) with FDR of rumen fluid 0-2 h and 2-7 h after feed was offered for both groups of animals. FDR before feeding described only 6 % of the variation in amount of foam produced 3 h before feeding.

The amount of foam produced was higher (P<.05) for the concentrate diet than for the hay and pellet diets 3 h before feeding (Table 2.3). No differences in foam heights were detected between diets at 4 h after feeding. Foam heights showed significant negative correlations (r -0.89 and -0.99 respectively; P<.05) with rumen-fluid FDR for all cattle given hay 2 h and 4 h after feeding (Table 2.4). However, for the pellet diet the correlation reached significance (r -0.89; P<.05) only at 2 h after feeding. For the concentrate diet, the correlation was significant (r -0.83; P<.05) only at 4 h after feeding (Table 2.4). There was a lack of significance between the correlations of rumen fluid FDR and amounts of foam produced from rumen contents 3 h before feeding in all diets.

Cattle in the different groups and cattle fed on different diets showed similar percentage decreases in foam heights 5 min after initial foam formation at both 3 h before and 4 h after feeding, therefore, only measurements made 2 h after feeding are shown (Table 2.3). There were no ($P>.05$) differences in foam instability between the two groups. Differences between the hay and pellet diet also lacked significance, although both diets resulted in less-stable foam ($P<.05$) than the concentrate diet. Rumen-fluid FDR during all the sampling phases described at most only 15 % of the variation in foam instabilities.

2.4 DISCUSSION

The decision to use cattle with previous histories of bloating only 3 months after rumen cannulation and to compare these with normal cattle which had been cannulated for 2 years and were larger was made deliberately to try to ensure that differences between the two groups of animals would exist. Because the groups of cattle were dissimilar it is not possible to make firm conclusions concerning the causes of bloating in cattle of group B, but relationships between the tendency of rumen contents to foam and the FDR of rumen fluid and particulate passage rate constants can be examined, and it would be expected that cattle with more foam in their reticulo-rumen contents would be more susceptible to bloat (Howarth et al. 1986).

The greater amount of foam produced by samples of rumen contents from cattle fed on the concentrate diet accords with reports of higher incidence of bloat in cattle when fed on combinations of lucerne hay and barley grain (Geissler and Thomas, 1966; Howarth, 1975).

Since there was no significant difference in foam instability between groups A and B, clearance of foam produced during and after feeding for a particular diet would be expected to be dependent on rumen-fluid FDR for that diet. Thus, in cattle with a significantly higher rumen-fluid FDR during and after feeding, e.g., group A of the present study, the accumulation of microbial and plant by-products, and therefore bloat, may be prevented. On the other hand, a lower rumen fluid FDR during and after feeding, such as in group B, may not be high enough to prevent such accumulations of stable foam and, therefore, bloat.

for the hay diet the FDR 0-2 and 2-7 h after feeding accounted for 79 and 98 % of the variation in amount of foam produced. Corresponding values for the pellet diet were 79 and 51 % respectively. Rumen-fluid FDR accounted for only 16 and 69 % of the variation in amount of foam produced 0-2 h and 2-7 h after feeding for cattle on the concentrate diet. The low correlation between FDR and foam production for the 0-2 h post-feeding sample for cattle fed on this diet is difficult to explain. However, it could be due to animal variability and the small number of animals involved in the present study, or it could indicate that for concentrate diets the relationship between FDR and foam production is more complex than for hay diets. For example, viscosity of rumen fluid has been shown to be positively correlated with the incidence of bloat in animals fed on a high grain diet (Meyer and Bartley, 1971). Also cattle spend less time eating a grain-based diet than a hay diet and saliva production during eating is less (Bartley, 1973). Reductions in anti-foaming salivary mucins entering the rumen and increases in mucinolytic bacteria in rumen fluid have also been reported in cattle fed on concentrate diets (Bartley and Yadava, 1961).

Across all diets the FDR 0-2 h and 2-7 h after provision of feed accounted for 55 and 72 % of the variation respectively, in the amount of foam produced from rumen contents of cattle. This suggests that the relationship between FDR and foam production holds under a variety of post-feeding situations.

Feeding caused a sharp decline in CoEDTA concentration (Figure 2. 1), a decline which could be related to the initial intake of the cattle after provision of fresh feed. Feeding causes declines in marker concentrations through expanded rumen volume or increased rate of passage or both (Warner and Stacy, 1968; Stokes et al. 1985).

The higher FDR for the hay diet 0-2 h after feeding could be attributed to increased mastication and salivation with the chopped hay as compared to the concentrate and pellet diets. However, when the cattle were no longer actively eating (2-7 h after provision of feed) the FDR was not significantly different between the animals given the chopped and pelleted hay diets.

The slower FDR of rumen fluid for group B at the various sampling phases are in agreement with the results of Majak et al. (1986b) who, during our analysis of the results from this study, reported first-order rate constants of 0.043 and 0.092 /h for bloat-susceptible and bloat-resistant cattle respectively. However, results in our study indicate that, although overall FDR may be important in explaining bloat differences, it may be more important to consider the relationships between the various components which contribute to the overall FDR and foam production. Thus, an overall slower FDR for group B could be attributed to significantly-slower rates of passage of CoEDTA during and after feeding and the concomitant higher foam production, but not to a slower FDR before feeding. It is during and after feeding that most animals normally bloat (Howarth, 1975).

Group B had significantly larger reticulo-rumen volumes than group A. Cockrem et al. (1983) reported significant differences in rumen volumes between high-susceptible and low-susceptible cattle and indicated that a greater volume of rumen fluid could be associated with a high susceptibility to bloat.

The mean fractional passage rates of the 1-2 mm Cr-mordanted particles, though higher in group A, were not significantly different from those of group B. Particles which could be responsible for frothiness by causing an increase in the viscosity of the lamellae fluid, thus preventing drainage of the fluid, as suggested by Majak et al. (1986a), could be smaller than 1 mm and thus would move with the liquid phase.

2.4.1 Conclusion

In conclusion, in the present experiment the study of animal factors involved in bloat susceptibility in cattle have been expanded to include the relationship between FDR of fluids before feeding, during feeding and after active feeding and the amounts of foam produced from rumen contents during these times. Cattle with previous history of being bloat-susceptible (group B) had greater foam productions from rumen contents and slower liquid FDR after feeding than cattle which were not bloat-susceptible (group A), whereas before feeding there was no significant difference in FDR and in amount of foam produced. The low FDR in group B could cause foaming agents to accumulate and account for increased tendency for animals to bloat.

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Table 2.1. FEED CONSUMPTION PATTERNS OF BLOAT-RESISTANT (group A) AND BLOAT-SUSCEPTIBLE (group B) CATTLE FED ON CHOPPED LUCERNE (*Medicago sativa*) HAY (hay) LUCERNE PELLETS (pellets) AND HIGH-BARLEY-GRAIN (concentrate) DIETS

(Means with pooled standard errors)

Group	A	B	SE*
Body-wt (kg)	539^a	386^b	10
Daily dry matter (DM) intake			
kg	13.0^a	10.0^b	.29
% body weight	2.4^a	2.6^a	.16
Mean initial DM intake†			
kg/d	5.2^a	3.8^b	.30
% body-weight	$.97^a$	$.98^a$	.04
Average DM size of meal‡			
kg/d	2.1^a	1.7^b	.05
% body-weight	$.39^a$	$.44^a$	.03

[a,b] Within rows, means with different superscript letters were significantly different (P<.05).

[*] SE of cattle group means (n = 9, df = 6).

†Intake after provision of fresh feed until animals left feedbunk.

‡Values obtained from total feed intake and number of visitations made to feed in an 8-12 h period.

Table 2.2. RUMEN DIGESTA KINETICS IN BLOAT-RESISTANT (group A) AND BLOAT-SUSCEPTIBLE (group B) CATTLE FED ON CHOPPED LUCERNE (*Medicago sativa*) HAY (hay) LUCERNE PELLETS (pellets) AND HIGH-BARLEY-GRAIN (concentrate) DIETS

(Means with pooled standard errors)

	Group			Diets			
	A	B	SE*	Hay	Concentrate	Pellets	SE†
Rumen volume							
Litres	87.9^{a}	95.6^{b}	1.20	97.1^{a}	87.8^{a}	90.0^{a}	3.1
% body-weight	16.3^{a}	23.3^{b}	11.0	20.9^{a}	18.9^{a}	19.4^{a}	1.0
Fluid dilution rate constant (/h)							
2.5-0 h before feeding	0.077^{a}	0.049^{a}	0.009	0.08^{a}	0.07^{a}	0.063^{a}	0.056
0-2 h after feed offered	0.205^{a}	0.093^{b}	0.007	0.173^{a}	0.13^{b}	0.145^{b}	0.004
2-7 h after feed offered	0.16^{a}	0.086^{b}	0.005	0.143^{a}	0.093^{b}	0.134^{a}	0.003
Fluid outflow rate (1/h)‡	7.4^{a}	4.5^{b}	0.50	7.9^{a}	6.0^{a}	5.6^{a}	0.54
Passage rate of 1-2 mm Cr-MP (/h)	0.067^{a}	0.050^{a}	0.012	0.047^{a}	0.072^{b}	0.055^{a}	0.002

[a,b] Within rows and comparisons, means with different superscript letters were significantly different ($P<.05$).

Cr-MP, Cr-mordanted particles.

*SE of cattle group means (n = 8, df = 6).

† SE of diet means (n = 6, df = 2).

‡Fluid outflow rate was estimated for the time period from 2.5-0 h before feeding.

Table 2.3. FOAM STABILITY AND FOAM HEIGHTS (mm) PRODUCED IN SAMPLES OF RUMEN CONTENTS TAKEN BEFORE AND AFTER FEEDING FROM BLOAT-RESISTANT (group A) AND BLOAT-SUSCEPTIBLE (group B) CATTLE FED ON CHOPPED LUCERNE (*Medicago sativa*) HAY (hay) LUCERNE PELLETS (pellets) AND HIGH-BARLEY-GRAIN (concentrate) DIETS

(Means with pooled standard errors)

	Foam heights (mm) at various times after feeding (h)			Foam instability[*]
	-3	2	4	
Group				
A	79^{a}	150^{a}	60^{a}	43^{a}
B	82^{a}	240^{b}	150^{b}	40^{a}
SE†	9.9	12.1	11.9	1.6
Diets				
Hay	32^{a}	148^{a}	76^{a}	54^{a}
Concentrate	122^{b}	236^{b}	135^{a}	22^{b}
Pellets	87^{c}	194^{ab}	102^{a}	50^{a}
SE‡	2.7	7.8	16.0	1.11

[a,b] Within column and comparisons, means with different superscript letters were significantly different ($P<.05$).

[*] Values represent the difference between initial foam height after gassing for 2 min and the foam height 5 min after gassing, expressed as a percentage of initial foam height measured 2 h after feeding.

† SE of mean (n = 9, df = 6).

‡ SE of mean (n = 6, df = 2).

Table 2.4. CORRELATION COEFFICIENTS (r) SLOPES AND INTERCEPTS OF LINEAR REGRESSIONS BETWEEN FOAM HEIGHTS (mm) AND RUMEN-FLUID DILUTION RATES (/h) AT VARIOUS TIMES AFTER FEEDING

		Time after feeding (h)		
Diet†	Item	-3	2	4
All diets				
	Intercept	8.77	27.3	18.0
	Slope	-0.18	-0.63	-0.63
	SE‡	0.18	0.14	0.096
	r	-0.24	-0.74*	-0.85*
Hay				
	Intercept	12.0	39.4	20.6
	Slope	-0.28	-1.49	-0.96
	SE‡‡	0.15	0.38	0.06
	r	-0.70	-0.89*	-0.99*
Concentrate				
	Intercept	6.33	8.5	17.1
	Slope	-0.05	-0.24	-0.55
	SE‡‡	0.40	0.85	0.19
	r	-0.30	-0.40	-0.83*
Pellets				
	Intercept	3.67	33.9	16.6
	Slope	-0.31	-1.00	-0.50
	SE‡‡	0.83	0.25	0.26
	r	-0.40	-0.89*	-0.72

† For details, see Page 24.

‡ SE of slope (n = 18, df = 16).

‡‡ SE of slope (n = 6, df = 4).

* P<.05

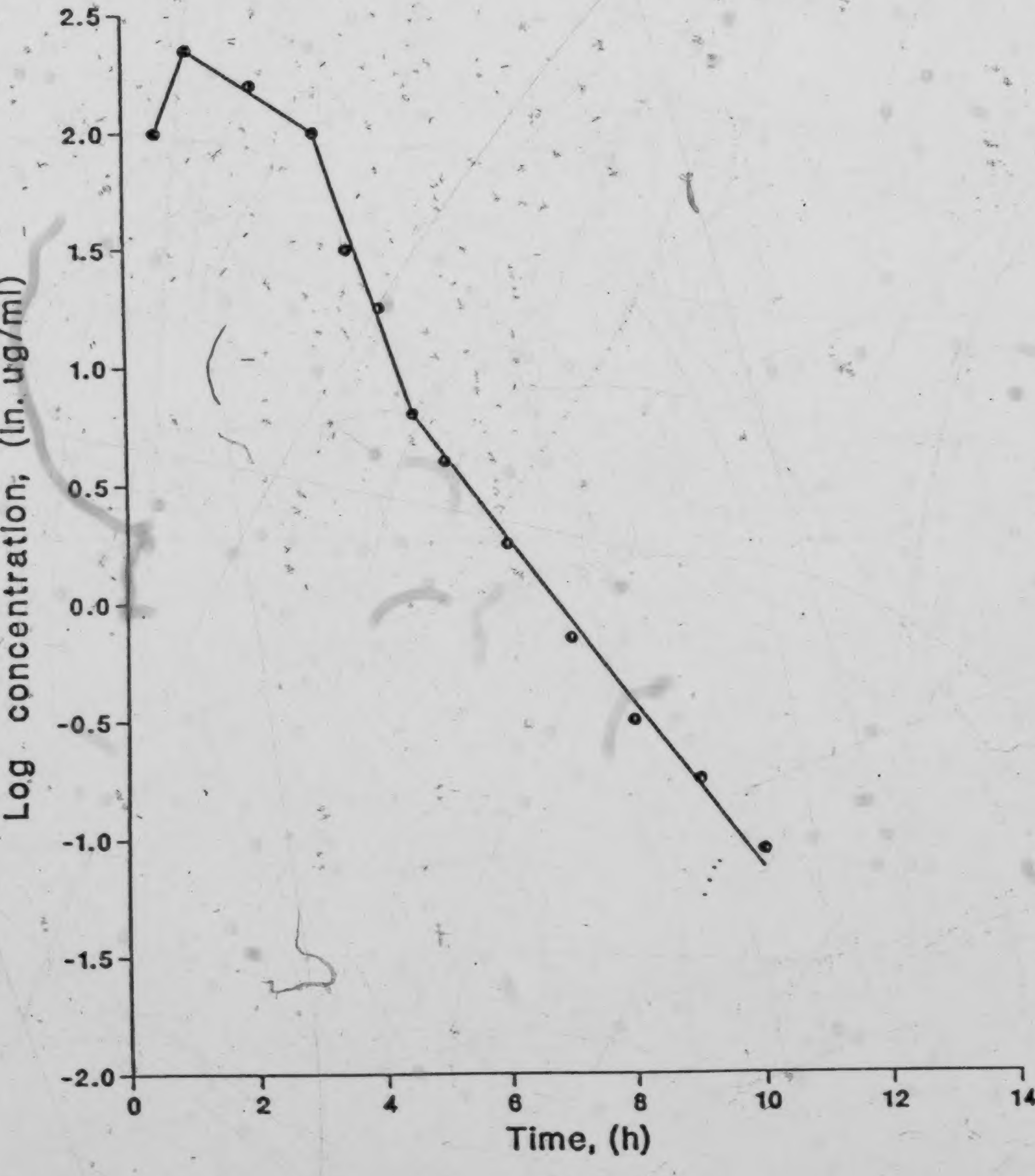
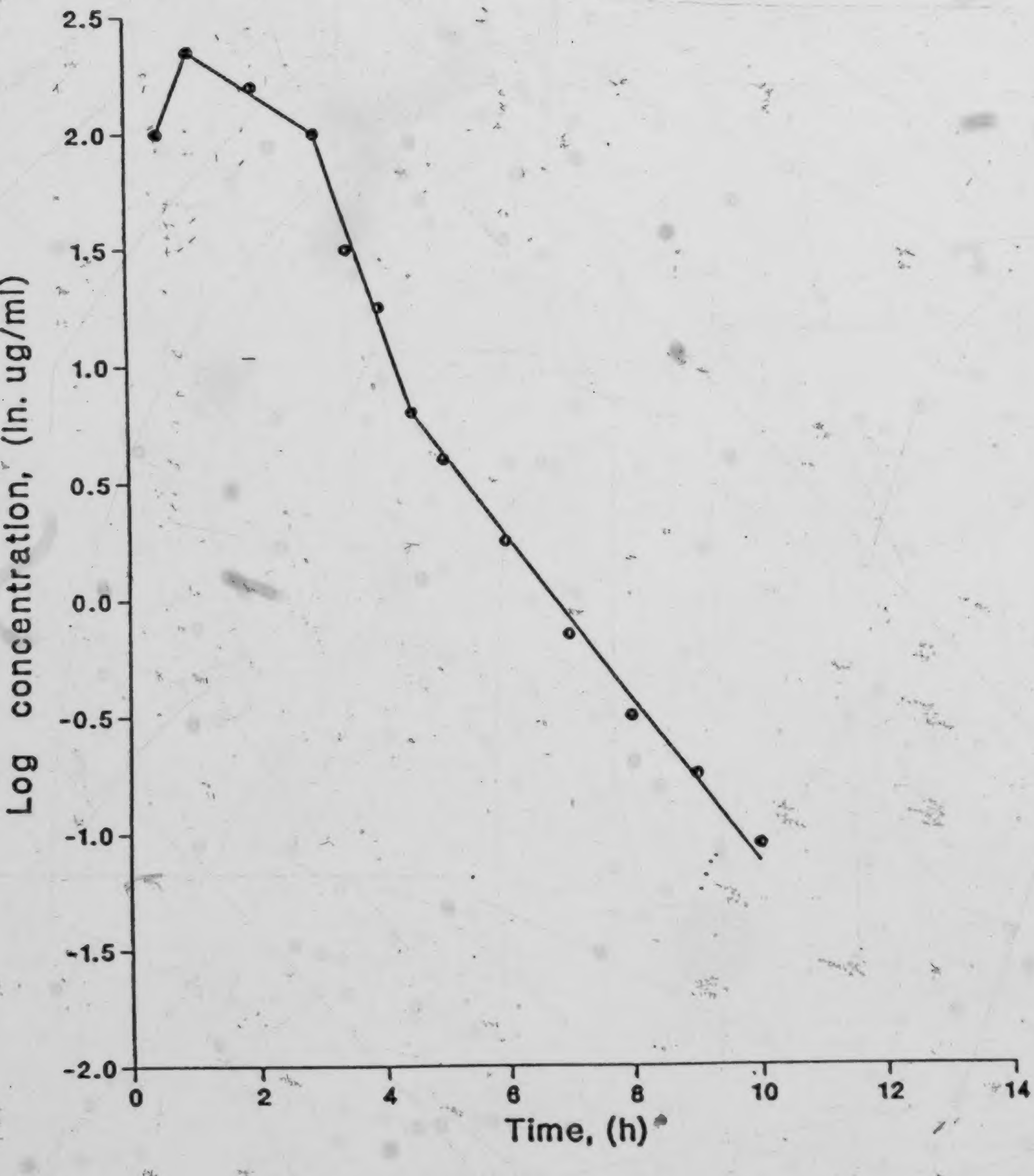

Log concentration, (ln. ug/ml)
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0
2
4
6
8
10
12
14
Time, (h)

Figure 2.1. Example of a multi-component marker-concentration curve of CoEDTA in the rumen of cattle. Marker was given 3 h before feeding.


2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Log concentration, (ln. ug/ml)
0
2
4
6
8
10
12
14
Time, (h)

III. EFFECTS OF CHANGES IN FREQUENCY OF RETICULAR CONTRACTIONS ON FLUID AND PARTICULATE PASSAGE RATES IN CATTLE[1]

3.1 INTRODUCTION

Passage of indigestible material from the rumino-reticulum (RR) to the lower gastrointestinal tract helps to negate the satiating influence of distension or volume of contents in the RR of ruminant animals given low quality forages (Mertens and Ely, 1982). Generally it is believed that an increase in the frequency of ruminoreticular contractions (increased rumen motility) leads to an increase in rate of passage of digesta from the rumino-reticulum (Reid, 1963; Sissons et al., 1984). Sarna (1985), however, suggests that changes in frequency of contractions may not change rate of transit.

It is known that increases in feed intake increase both frequency of reticular contractions and passage rates (Grovum, 1986). The higher feed intakes, however, are associated with larger volume (Grovum, 1984) and weight (Leek, 1987) of RR contents, both of which are associated with increases in frequency of reticular contractions.

The objective of this study was to determine the effects of weights in the rumen on frequency of reticular contractions in animals at a maintenance feed intake and on the passage rates of both fluid and particulate matter from the RR and from the total gastrointestinal tract. Duration of reticular contractions, apparent digestibilities and heat and methane productions were also determined.

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[1] A version of this chapter has been published. Okine, E.K., G. W. Mathison and R.T. Hardin. 1989. J. Anim. Sci. 67:3388-3396.

3.2 MATERIAL AND METHODS

3.2.1 Experimental design

Four Hereford steers (531 ± 32 kg) which had been ruminally cannulated 1 year previously were used in a double crossover design experiment. The experiment consisted of four periods, with steers having no weights (control; C) or 24 kg weights (W) in the rumen in alternate periods. Each period consisted of 23 d with two steers with weights and two steers without weights in the rumen starting each period. The weights consisted of a total of six wide-mouth high-density polyethylene containers (17.8 x 8.9 x 8.9 cm) with polypropylene screw tops filled with sand, which were tied with 10 cm lengths of polypropylene twine around the circumference (.94 m) of semi-flexible plastic hose (2.5 cm o.d.). The adaptation time of the steers to the weights in the ventral sac of the rumen in each period was 14 d.

3.2.2 Feed

The diet used in this experiment consisted of a 50%:50% mixture (dry matter (DM) basis) of bromegrass (Bromus inermis) and alfalfa (Medicago sativa) hays ground to approximately 6 cm through a tub grinder[2] which contained 91% OM, 57.3% NDF, 43.6% ADF, 11.5% CP and 8.7% ADL on a DM basis. The steers, maintained indoors in individual metabolic stalls with continuous lighting at an ambient temperature of 20-22°C, were fed at a calculated maintenance feeding level with the ration being offered twice daily at 0900 and 1600 with the first allotment being 50% of the total. Trace mineralized salt blocks[3] and water were available free choice except during the indirect calorimetry studies where water was provided in buckets after feeding.

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[2] Model 390, Sperry New Holland, PA.

3.2.3 Passage rate studies

The particulate marker used for rumen and total tract particle passage rates (PPR) was chromium mordanted to NDF of the mixture of brome grass and alfalfa hays according to the method of Uden et al. (1980). Particles contained 4% Cr after mordanting. Ruminal fluid dilution rates (FDR) were determined using crystalline Co-EDTA prepared according to the procedures of Uden et al. (1980).

The animals were dosed intraruminally with markers (5 g of Co and 4 g of Cr) simultaneously at 0600 on d 15 for both FDR and PPR studies, 3 h prior to feeding. In this procedure approximately half the rumen contents were removed, mixed with Co-EDTA and Cr-mordanted particles and returned to the rumen. Ruminal fluid for fluid dilution rate determinations was sampled from the reticulum, and the dorsal, ventral and caudal sacs of the rumen at 1 h intervals until 15 h post-dosing. Contents were squeezed through four layers of cheesecloth, the filtrate was frozen and the solid particles returned to the rumen. Samples for solid particle passage rate determinations were taken from the top and bottom of the reticulum, the ventral and dorsal sacs and caudal sac at 3, 6, 9, 12, 18, 26, 30, 36, 50 and 75 h after administration of the mordanted particles. Samples were mixed, subsampled and frozen for subsequent analyses. Fecal samples for gastrointestinal passage rate studies were collected at 3, 6, 9, 12, 15, 18, 26, 30, 33, 36, 42, 50, 54, 60, 75, 84, 98, and 108 h after administration of the mordanted particles. Fecal collection at each time was the total amount produced since the previous collection. Feces were thoroughly mixed, subsampled and frozen until analyzed. Prior to analyses for marker concentrations 50 g of fecal and rumen samples were oven dried for 3 d at 60°C and ground to pass a 1 mm screen. The passage rate constants for each marker were calculated as first-order constants since first-order kinetic equations described more than 90% of the variance in the decline in concentration of each marker with time in twelve out of the sixteen situations. Separate regressions were employed to calculate the FDR constants during each sampling phase: before feeding and during and after feeding. Initial rumen weight of particles and fluid volume were calculated from the added weights of Cr-mordanted fiber and Co-EDTA, respectively, and the concentration of the marker at zero time was estimated by extrapolation of the natural logarithm of concentration using regression points before feeding (Okine et al. 1989).

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[3] Composition:>95% NaCl, .25%Mn, .2%Fe, .03%S, .003%Cu, .007%I and .005%Zn.

3.2.4 Apparent digestibility studies

Fecal samples collected during the period of passage rate studies also were used for digestibility determinations. Fecal samples collected at intervals of 3, 6, 9, 12, 15, 18, 26, 75, 84 and 98 h, were bulked, subsampled and analyzed for apparent digestibilities of DM, CP, OM, NDF, ADF and energy using ADL as an internal marker (Merchen, 1988).

Dry matter was determined by drying at 110°C in a forced-air oven to a constant weight. Crude protein was determined by the Kjeldahl method for nitrogen according to AOAC (1980) using method 2.057. Organic matter was determined by ashing a dried sample at 550°C (AOAC 1980, method 2.176). Neutral detergent fiber, ADF and ADL were determined using the methods described by Van Soest and Robertson (1980). Gross energy content of feed and feces was determined by bomb calorimetry using an automatically controlled Parr adiabatic bomb calorimeter[4].

3.2.5 Methane and heat production

The indirect calorimetry method utilizing a hood collection system was used to measure methane and heat production on d 21 and 22. Oxygen consumption and respired gases (methane and carbon dioxide) were measured on four animals simultaneously with an open circuit calorimeter system similar to that described by Young et al. (1975) except that the system was automated and Foxboro orifice plate flow transmitters[5] were used to measure gas flow and gas pressure was measured with a Foxboro absolute pressure transmitter[6].

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[4] Model 1241, Parr Instrument Co., Moline, IL.
[5] Model 823DP, Foxboro, MA.
[6] Model 821AL, Foxboro, MA.

Loss of gas from the rumen fistulas was minimized in this study by positioning a plastisol washer around the cannula body to hold the cannula body against the rumen wall of each animal. The equations of Brouwer (1965), without consideration of urinary nitrogen excretion, were used to calculate heat production.

3.2.6 Motility studies

Reticular contractions were measured in four steers following the methods of Froetschel et al. (1986). Briefly, a fluid filled open tipped catheter (polyvinylchloride, .09 mm i.d.) was inserted into the reticulum and connected to a pressure transducer[7] and a Beckman physiological recorder[8]. Weights (40 g) were fixed 15.0 cm from the anterior portion of the catheter to ensure that catheter remained in the reticulum. Pressure transducers were maintained at a height that was level with the tip of the catheter. Water (2.5 ml/min) was infused into the catheter tube using a continuous infusion pump[9] to prevent rumino-reticulum digesta from entering the catheter. On d 23 of each period, reticular contractions, were measured at prefeeding (0800 to 0900), feeding (0900 to 1000) and post-feeding (1000 to 1100) phases of the feeding cycle. The frequency and duration of reticular contractions were obtained by counting the number of reticular contractions and by measuring the horizontal distance between the beginning and the end of the second reticular contraction, from physiological tracings. The frequency and duration of the reticular contractions were averaged over the 60 min measuring period of each phase of the feeding cycle.

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[7] Model P23DB, Gould Statham, CA.

[8] Model R-612, Electronic Division, IL.

[9] Model MP-13G54, SA. Zurich.

3.2.7 Statistical analyses

The data for the pre-feeding, feeding and post-feeding phases of each feeding cycle were analyzed using regression and analyses of variances (Steel and Torrie, 1980). Analyses of variance for main effects only were computed using the Statgraphics (STSC Inc., Rockville, MD) multifactor ANOVA program, with eight degrees of freedom (df) in the error term, and animals (df = 3), ruminal weights (df = 1) and periods (df = 3) as main sources of variation. Means are shown with pooled SE's and were compared using Tukey's range test (Steel and Torrie, 1980). Preliminary analysis of covariance (Steel and Torrie, 1980) indicated no significant ($P > .05$) differences in the relationships between methane production and flow rate constants due to periods, animals or weight. Therefore, the overall simple regressions of methane production on the different flow rate constants were deemed as valid and were computed.

3.3 RESULTS

3.3.1 Motility Studies

The frequency of reticular contractions before feeding was not affected (P = .07) by adding weights to the rumen. However, the frequencies of reticular contractions for steers with weights in the rumen during the feeding and post-feeding phases were 14 and 8% lower (P = .03; P = .05), respectively, than contractions for steers without weights in the rumen (Table 3.1). Addition of weights to the rumen resulted in increases (P = .04; P = .01; P = .05) of 12, 15 and 15% in the duration of reticular contractions before feeding, during feeding and after feeding, respectively (Table 3.1).

3.3.2 Passage rate studies

Mean RR fluid volume was 19% lower (P = .001) in C vs W steers (Table 3.2). Rate constants for the passage of Co-EDTA from the rumen before feeding were 25% (P = .003) and 30% lower (P = .005) during and after feeding in C vs W steers (Table 3.2). Mean RR particulate weight was not different (P = .067) between C and W steers. The rate constants for passage of Cr-mordanted fiber from the rumen and through the total gastrointestinal tract were 38% and 49% lower (P = .001), respectively, in C vs W steers (Table 3.2). There was a significant relationship between ruminal passage rate constants (Y) and gastrointestinal passage rate constants (X) ($Y = .0057X + .0138$; n = 16; P = .006; SE = .0018).

3.3.3 Apparent digestibilities

Apparent digestibilities of feed components did not differ between W and C steers (P = .76) (Table 3,3).

3.3.4 Methane and heat productions

Addition of weights to the rumen had no significant effect (P = .140) on the heat production of the steers (12.3 and 12.6 Mcal/d for steers with and without weights, respectively) (Table 3.4). Adding weights to the rumen decreased (P = .001) methane production by 29% (Table 3.4). Methane productions (liters/d) were negatively correlated (r = -.53; P = .034) with passage rate constants for ruminal particulate matter, and also were inversely related (r = -.50; P = .033) with ruminal fluid dilution rates during the feeding and post-feeding phases of the feeding cycle (Table 3.5). However, methane production was not related (r = -.22; P = .420) with ruminal fluid dilution rates before feeding (Table 3.5).

3.4 DISCUSSION

3.4.1 Ruminal Contractions

The motility of the RR and passage of digesta out of the rumen are important aspects of rumen function and their significance in quantitative terms to volume of rumen digesta and increased intake continue to be systematically investigated (Colucci et al. 1982; Grovum, 1984). High feed intakes which give rise to increased volume of digesta in the rumen must necessarily lead to increased weight of digesta in the rumen. In addition, cattle fed a diet containing a high proportion of a poor quality forage have a greater weight of digesta in their RR than cattle fed concentrate-based diets (Bines and Davey, 1970). Investigation of the contribution of weight of rumen digesta, as distinct from the bulk of digesta, to the motility of the RR and passage of digesta from the rumen has, however, been neglected. The decision to add weights to the rumen was therefore made in order to provide information on the relationship between RR motility and various aspects of digestive function without the confounding effects of increased volume of rumen digesta and high feed intakes. Weights of 24 kg were chosen deliberately to ensure that differences between the two groups would exist.

It was recognized that addition of weights to the rumen might lead to artificial physiological conditions in the RR. A persistent discharge of the epithelial mechanoreceptors due to extreme mechanical stimulus, resulting in greater inhibitory effects on reticular contractions (Leek, 1987), could be an example of such an artificial state. In spite of this concern it is believed that the addition of weights to the rumen provided a useful method of changing RR motility without changing other aspects of the physiology of the animals, as for example, would occur with changes in feed intake.

Steers with weights had 14 and 8% lower frequencies of reticular contractions during the feeding and post-feeding phases of the feeding cycle, respectively. This was in contrast to expected results. Reid (1963) reported that for a given animal and feed, there was a positive relationship between the amount eaten and both the extent and persistence of increases in frequency of RR contractions. Grovum (1986) also reported a 46% increase in frequency of reticular contractions during feeding relative to the fasted state. Feeding passively distends the RR with ingesta and gases and enhances motility, presumably through activation of the slowly-adapting tension receptors. In contrast, in our studies, the lower frequency of reticular contractions in W steers could be due to reflex inhibition arising from excessive stimulation of the epithelial mechanoreceptors by the weights which settled on the floor of the ventral sac of the rumen. This could have caused persistent discharge of these receptors with subsequent greater inhibitory effects on reticular contractions (Leek, 1987).

Sissons et al. (1984) reported positive relationships between frequencies of reticular spike-bursts and turn-over rates of liquid ruminal digesta. The present results indicate that even though adding weights to the rumen significantly increased both fluid dilution rates and particulate passage rate constants, the steers with weights had significantly lower frequency of reticular contractions. Increased frequencies of contractions then could not have been the cause of the increase in passage rate constants. Other characteristics of motor activity such as amplitude of contraction, the duration of contraction, the coordination of these events and the opening of the reticulo-omasal orifice that help to determine propulsion have been identified (Reid, 1963), and it may be the combined effects of these that determine the rate of propulsion of RR contents and not frequency of contraction alone per se. Weights in the rumen increased the duration of reticular contractions by 12, 15 and 15% before feeding, during feeding and post-feeding phases of the feeding cycle. Since the reticulo-omasal orifice remains open during the biphasic reticular contractions (Ohga et al., 1965 quoted by Grovum, 1986), the increased duration of the reticular contractions may be the cause of the increased passage rates of both ruminal fluid and particulate matter found in this study. Although amplitudes of contractions were not determined in this study due to technical difficulties, preliminary indications from a subsequent study indicate that the addition of weights to the rumen had a greater effect on the duration of reticular contraction than it had on the amplitude of contraction (chapter IV).

3.4.2 Apparent digestibility of feed components

Incomplete recoveries of fecal lignin (Fahey and Jung, 1983) may have masked any potential differences between the treatments and also may have resulted in the rather low digestibilities calculated in this study. However, the relative values were still deemed useful since the emphasis was on comparing digestibility coefficients and not on the absolute digestibilities of the nutrients per se. Passage rates and digestibilities are expected to change in opposite directions so that an increase in passage rates leads to a decrease in digestibility (Kennedy and Milligan, 1978; Colucci et al., 1982). Kennedy and Milligan (1978) reported that an increase of 54% in passage rate in cold-adapted sheep fed bromegrass led to a 10% decrease in DM digestibility. Results of this experiment showed no differences between steers with and without weights in the rumen with reference to digestibility coefficients, although steers with weights had significantly higher passage rate constants of Cr-mordanted fibers from the rumen and through the total gastrointestinal tract.

The physical form of forages fed is an important factor in determining the extent of depression in digestibility with increases in passage rates. The feed fed in this experiment was a 50%:50% mixture of alfalfa and bromegrass with relatively large particles and, as Alwash and Thomas (1971) pointed out, an increased intake of chopped grass from maintenance to three times the maintenance feeding level with an increase of 78% in passage rate led to only a 2.8% depression in crude fiber digestibility. However, feeding ground and pelleted grass at the high intake level, with an increase of 64% in the passage rate constant, led to a 35% depression in crude fiber digestibility. Merchen (1988) suggests that the minimal ruminal retention time required for reduction in the particle size of forages fed in either the long or chopped forms to sizes small enough to exit the RR is probably long enough to ensure extensive breakdown of the digestible portion of the feedstuff. This phenomenon could account for the relatively small depression in digestibility of long and coarsely chopped forages with increased passage rates. The low feed intakes (1.4% of BW) maintained for both groups of animals in this study could also have precluded any significant differences in the extent of depression in digestibilities of various components of the diet. Robinson et al. (1987) reported increases in rate of digestion with decreases in intake. Such an increase in the rate of digestion could have caused any depression in digestibility due the increased passage rates with the addition of weights to the rumen to be insignificant. The negligible effect of passage rate on digestibility could also have been due to post-ruminal compensatory digestion, which can be significant when digestion in the RR is incomplete (Hoover, 1978).

3.4.3 Methane and heat production

Methane productions reported in this study were estimates of rumen methane production since post-rumen methane production was not measured. Kennedy and Milligan (1978) reported that post-rumen methane production accounted for 23% of the total methane produced in sheep. The 29% decrease in methane production (liters/d) of the steers caused by addition of weight to the rumen was related to a 39% increase in fractional passage rate of the Cr-mordanted fiber from the rumen and a 30% increase in rumen fluid dilution rate. This is consistent with reports of a 30% decline in methane production with 54 and 68% increases in ruminal passage rate constants of fluid and particulate matter in cold-adapted sheep at a constant intake (Kennedy and Milligan, 1978). The overall relationship between methane production and ruminal particulate matter passage rate constants was found to be negative (P = .034), with the passage rate constants explaining 28% of the variation in methane production. Ruminal fluid dilution rates during feeding and after feeding explained 25% of the variation (P = .033) in methane production. Although measurement of ruminal volatile fatty acid concentrations was not made, decreased methane productions associated with the increased passage rates of both ruminal fluid and particulate matter from the rumen at a constant feed intake as seen in this study may indicate a partial shift from a methanogenic fermentation to a propionate type fermentation in the rumen (Fahey and Berger, 1988). The reduced methane energy per unit of intake energy is similar to results in dairy cows with increased intakes (Moe and Tyrrell, 1979). However, whereas in this study animals with weights in the rumen had a significantly lower methane production (liters/d), Moe and Tyrrell (1979) reported higher methane production in cows at high intakes than at low intakes. Normally, increased methane production with intake is due to increased fermentation of nutrients since the animals consume additional nutrients, whereas in this study only weights were added. Blaxter and Clapperton (1965) showed that methane production in sheep was positively related to the digestibility of dietary energy and negatively related to the level of feeding. However, their prediction equations would not apply to the present work since both digestibility of dietary energy and the DM intakes were constant across the treatment groups.

The results of this experiment suggest that adding weights to the rumen did not increase heat production and if anything, decreased (P = .14) heat production of the steers. These results were contrary to those expected since the increase in weight of RR contents from the added weights and increased digesta load was 36.4 kg (Table 3.2). It is known that cattle fed a diet containing a high proportion of a poor quality forage have a greater heat increment of feeding (Kellner, 1926 quoted by Webster, 1980) and a greater weight of digesta in their RR than cattle fed concentrate-based diets (Bines and Davey, 1970). With the portal-drained viscera reported to utilize up to 29% of the total amount of oxygen utilized by the animal (Huntington et al., 1985), and since the amount of oxygen consumed by this organ increases with intake (Webster et al., 1975), it was expected that the addition of weights to the rumen could lead to variations in energy expenditure of the animals. The results from the present study are equivocal also because Adam et al. (1984) demonstrated that increases in energy cost of eating are more of a function of time spent eating than the amount of feed ingested, and it was observed that steers with weights in the rumen spent 1.5 h eating at each feeding period compared 45 min for steers without weights in the rumen. However, Engelhardt and Hales (1977) concluded that a very high proportion (95%) of blood flow to the forestomach was directed to the mucosa and this reflected the importance of absorption and metabolism as the primary source of heat production in contrast to the physical work done by the muscle of the RR which only accounted for 5% of the total blood flow. Thus, although weights in the rumen probably led to a small increase in physical work by the muscle of the RR, its effect on heat production was insignificant. In addition, changes in heat production caused by absorption and metabolism in the mucosa of the RR may not have been significant because of the rather low intake of feed (1.4% of BW) maintained in this study. Also, a shift of site of digestion postruminally, as indicated by the 56% higher ruminal particulate outflow in W steers, would change the efficiency of energy use (Beever et al., 1972).

3.4.4 Conclusion

In conclusion, this study showed that, in contrast to the reports of Reid (1963), and Sissons et al. (1984), increases in fractional passage rates of both ruminal fluid and particulate matter are not necessarily due to increases in frequency of reticular contractions. Changes in the other indices of ruminal motility, such as increases in the duration of reticular contraction, appear to be more important in effecting increases in passage rates. The significant inverse relationships between passage rate constants of both ruminal fluid and particulate matter as independent variables and methane production confirm that passage rates have an effect on methane production which independent of intake and diet composition. Finally, it was determined that increased weight of material in the rumino-reticulum is not the cause of the relatively high heat increment of feeding which is observed when forages are fed. Further work to ascertain the relevance of amplitude, duration and frequency of reticular contraction on motility has been undertaken (chapters IV and V).

3.4.5 Implications

Results imply that of flux of digesta through the reticulo-omasal orifice can increase despite a decrease in frequencies of reticular contractions. An increased duration of reticular contraction potentially increases passage rates. Increased weight in the rumen had no effect on heat production, so the increase in heat increment of feeding when animals are fed roughages rather than concentrates is not due to differences in weight of digesta in the rumen; other factors such as nutrient metabolism and chewing activity presumably are responsible. Passage rates of ruminal digesta can be increased without decreasing digestibility. The significant inverse relationship between passage rates and methane production provides a direction for further research to ascertain the relevance of passage rates of digesta on rumen function.

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Table 3.1. EFFECTS OF 24 KG WEIGHTS IN THE RUMEN ON FREQUENCY AND DURATION OF RETICULAR CONTRACTIONS OF STEERS DURING PRE-FEEDING, FEEDING AND POST-FEEDING PHASES OF THE FEEDING CYCLE

Item	Without weights (C)	With weights (W)	SE[a]	Probability
Contraction frequency, min^{-1}				
Pre-feeding	1.1	1.0	.034	.07
Feeding	1.4	1.2	.035	.03
Post-feeding	1.2	1.1	.022	.05
Duration of contraction, sec				
Pre-feeding	4.9	5.5	.190	.04
Feeding	5.4	6.2	.103	.01
Post-feeding	5.3	6.1	.163	.05

[a] Pooled SE (8 df) with eight observations per mean.

Table 3.2. PASSAGE RATE CONSTANTS FOR FLUID AND PARTICULATE MARKERS FROM THE RUMEN AND THROUGH THE TOTAL GASTROINTESTINAL TRACT OF STEERS WITH OR WITHOUT 24 KG WEIGHTS IN THE RUMEN

Item	Without weights (C)	With weights (W)	SE[a]	Probability
Animal weight, kg	531	531		
Dry matter intake, kg/d	7.38	7.38		
Material in rumen				
Fluid, liters	55.2	67.8	1.41	.001
Fluid, liters/100 kg BW	10.5	12.9	.28	.001
Particulate matter, kg	2.90	2.72	.487	.067
Flow from rumen, h^{-1}				
Fluid before feeding	.083	.111	.005	.003
Fluid during and after feeding	.093	.133	.007	.005
Particulate matter	.024	.039	.002	.001
Flow through total GIT,[b] h^{-1}				
Particulate matter	.021	.041	.002	.001

[a] Pooled SE (8 df) of the mean with eight observations per mean.

[b] Passage rate constant for total gastrointestinal tract estimated from fecal samples.

Table 3.3. APPARENT DIGESTIBILITY COEFFICIENTS(%) FOR STEERS WITH OR WITHOUT 24 KG WEIGHTS IN THE RUMEN

Item	Without weights (C)	With weights (W)	SE[a]	Probability
Dry Matter	47.8	47.3	1.16	.79
Energy	48.5	47.9	1.22	.76
Organic Matter	52.1	51.7	1.17	.79
Neutral detrgent fiber	45.1	44.7	1.20	.85
Acid detergent fiber	40.8	41.0	1.20	.90
Crude protein	45.4	45.6	1.60	.91

[a] Pooled SE (8 df) with eight observations per mean.

Table 3.4. EFFECTS OF ADDED 24 KG WEIGHTS IN THE RUMEN ON HEAT AND METHANE PRODUCTIONS OF STEERS

Item	Without weights (C)	With weights (W)	SE[a]	Probability
Heat production				
Mcal/d	12.6	12.3	.14	.140
$Kcal \cdot d^{-1} \cdot (kg^{.75})^{-1}$	114.8	110.1	1.20	.096
Methane production				
liters/d	188.8	134.6	7.8	.001
Mcal/Mcal gross energy intake	.057	.040	.003	.001

[a] Pooled SE (8 df) with eight observations per mean.

TABLE 3.5. REGRESSION EQUATIONS RELATING METHANE PRODUCTIONS (Y; LITERS D^{-1}) TO RUMINAL PARTICULATE MATTER PASSAGE RATE CONSTANTS, OR RUMINAL FLUID DILUTION RATES BEFORE FEEDING, DURING AND AFTER FEEDING (X; H^{-1})

	Intercept	Slope	SE[a]	r	Probability
Particulate matter	201.5	-14.69	6.27	-.53	.034
Fluid dilution rates					
Before feeding	202.4	-4.25	5.12	-.22	.420
During and after feeding	211.7	-5.01	2.10	-.50	.033

[a] SE of the slope (n - 16, df - 14).

IV. EFFECTS OF CHANGES IN ATTRIBUTES OF RETICULAR CONTRACTION ON FECAL PARTICLE SIZES IN CATTLE[1]

4.1 INTRODUCTION

Increases in fractional passage rates of digesta from the rumino-reticulum (RR) have generally been associated with increases in frequency of reticular contractions (Sissons et al. 1984). Recent evidence however, suggests that changes in fractional passage rates of both fluid and particulate matter and increased outflow rates from the RR may not directly be related to changes in frequency of reticular contractions (Ulyatt et al. 1984; Bosch et al. 1988; Okine et al. 1989). Okine et al. (1989) reported that even though frequency of reticular contractions decreased as a result of addition of 24 kg weights to the rumen, particulate passage rate constants increased by 63% and rumen fluid passage rates constants increased by 34 and 43% during the pre-feeding and post-feeding phases of the feeding cycle, respectively. Changes in both particulate and rumen fluid passage rate constants were however, related to the duration of reticular contractions (Okine et al. 1989). The results of that study were not conclusive, however, since the amplitudes of contraction were not measured which together with the duration of reticular contractions, could determine the amount of digesta leaving the RR per contraction.

Increases in intake and passage rates have been associated with passage of fecal particle with larger mean size (Van Soest 1982; Deswysen et al. 1987; Van Soest et al. 1988). However, Waghorn et al. (1986) reported that intake level had no effect on omasal and abomasal particle size. Since changes in passage rate and intake are linked it is impossible to determine if increased passage rates per se caused increased fecal particle size or if particle sizes were related to other consequences of the increased intake. Since attributes of RR contraction can be affected at a constant feed intake by adding weights to the rumen (Okine et al. 1989), this effect can be used to separate the effects of feed intake and of RR contraction attributes on fecal particle size distributions.

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[1] A version of this chapter has been published. Okine, E.K., G.W. Mathison, and R.T. Hardin. 1990. Can. J. Anim. Sci. 70:159-166.

The objectives of this study were to determine if adding weights to the rumen changed the amplitude as well as the frequency and duration of RR contraction and to examine the relationships between RR contraction attributes and the particle size distribution in fecal material.

4.2 MATERIALS AND METHODS

4.2.1 Animals and feeds

Three ruminally-cannulated Hereford steers (605 ± SD 98 kg) were used in a 3 x 3 latin square design experiment. Each period consisted of 10 d during which steers, maintained indoors in individual pens with continous lighting at an ambient temperature of 20-22°C, had 0 (control; C), 9 (low weight; LW) or 18 (high weight; HW) kg weight in the ventral sac of the rumen. The weights consisted of three (9 kg) or six (18 kg) individual wide mouth high-density polyethylene containers (8.9 x 8.9 x 17.8 cm) with polypropylene screw tops filled with sand. The adaptation time of the steers to the weights in the ventral sac of the rumen was 6 d based on feed intake returning to normal after addition of the weight. The diet consisted of a 30:30:40: mixture of bromegrass (Bromus inermis), timothy (Phleum pratense) and alfalfa (Medicago sativa) hay which contained 92% OM, 55.4% NDF, 44.6% ADF, 11.0% CP and 9.1% acid detergent lignin (ADL) on a DM basis. The steers were fed at a calculated maintenance feeding level with no feed refusals with the ration being offered in equal amounts of 5 kg DM twice daily at 0900 and 1600 h. Trace mineralized salt and water were available free-choice.

4.2.2 Fractionation of particles

On d 7 to 9 of each period, fecal samples were collected at 0800 h by the rectal grab method. The fecal samples were fractionated into various particle size groups using a wet sieving procedure. The sieving apparatus consisted of a cylinder (110 mm diameter) with a removable screen at one end. The cylinder was placed in a beaker (180 mm diameter) to which 2.5 L tap water was added. The sample (approximately 10 g (DM)) was placed inside the cylinder and the slurry manually stirred in a rotary fashion using a spatula while the cylinder was slowly lifted within the beaker. The up-and-down movement with stirring was carried out six times using the same water and the particulate material retained on the screen was quantitavely transferred to a dish for DM determination. The slurry that passed through the first screen (6800 μm) was subsequently sieved using screens with mesh openings of 3200, 2500, ~~1000,~~ 500, and 250 μm in succession. Residues passing through the smallest screen were dried and weighed after centrifugation (14000 g, for 15 min.). Data for the particles on each screen were expressed as a percentage of the total DM collected on the screens. Cumulative percent of fecal DM retained on each screen was fitted to the log normal distribution as described by Waldo et al. (1971), and the geometric means and standard deviations were calculated. To determine the geometric mean particle diameter on the largest screen, an upper screen mesh opening of 13600 μm was assumed.

4.2.3 Motility studies

On d 10 of each period, the frequency and duration of reticular contractions were measured following the methods of Okine et al. (1989) during the feeding phase of the feeding cycle. In addition, amplitudes of reticular contractions were calculated using the standardized displacement caused by the application of a known pressure (measured by a mercury manometer) across the transducer as a reference. The frequency, duration and amplitude of reticular contractions were each averaged over the 1.5 h data collection period during the feeding phase of the feeding cycle.

4.2.4 Statistical analyses

Although the experiment was designed as a 3 x 3 latin square, preliminary analyses of variance of the data (Montgomery 1984) indicated no significant differences at ($P = 0.25$) for either periods or animals. The lack of significance at ($P = 0.25$) for animals and periods for all traits satisfied the requirements for pooling mean squares recommended by Montgomery (1984). For all traits the mean square for animals, period and the residual were pooled to provide a more reliable ($df = 6$) estimate of error. Therefore the final analyses of variance computed consisted of treatment (ruminal weights, $df = 2$) and error ($df = 6$). Effects of weights placed in the ventral sac of the rumen were determined using orthogonal polynomials (Steel and Torrie 1980). Relationships between reticular contraction attributes and distribution of different size fecal particles and geometric mean sizes were examined by regression analyses. Two-tail t-tests were used to determine the significance of the slopes.

4.3 RESULTS

4.3.1 Reticular contraction attributes

Addition of 0, 9 and 18 kg weights to the rumen resulted in a linear increase ($P = 0.04$) in the duration of reticular contractions (Table 4.1). These weights tended ($P = 0.08$) to linearly decrease corresponding amplitudes of contraction but quadratic ($P = 0.14$) effects were not significant (Table 4.1). Frequency of reticular contraction showed a quadratic effect ($P = 0.07$) with values of 1.4 min^{-1}, 1.7 and 1.6 min^{-1} for C, LW and HW steers, respectively, (Table 4.1).

The product of amplitude and duration (AxD) which could determine the amount of digesta leaving the RR per contraction, showed a linear increase ($P = 0.05$) (Table 4.1). The product of frequency and duration (FxD) of reticular contractions which indicates the total duration of reticular contraction per min. also showed a linear increase ($P = 0.04$) with the addition of weights to the rumen. However, the product of frequency and amplitude (FxA) of reticular contractions which determines the total pressure exerted during reticular contractions per min. showed a quadratic effect ($P = 0.09$) with values of 15.8, 18.5 and 16.8 mm Hg per min. for steers with increasing weights in the rumen (Table 4.1). Addition of 0, 9 and 18 kg weights to the rumen increased ($P = 0.06$) the combined effect of frequency, amplitude and duration (FxAxD) of reticular contractions (Table 4.1).

4.3.2 Particle size distribution

The proportion of fecal matter retained on the 6800 μm screen (0.1-0.3%) did not differ (P = 0.70) among treatments (Table 4.2). However there were linear increases in the proportion of particles retained on the 3200μm (P=0.01) and 2500μm (P =0.007) screens as well as quadratic increases (3200μm: P = 0.05; 2500μm: P = 0.04) with increasing weights in the rumen (Table 4.2). The proportions of particles retained on the 1000, 500, and 250 μm screens did not change with addition of weights to the rumen nor did the proportions of the residual particles (Table 4.2). With the current sieving techniques, cattle fecal matter retained on the 6800 and 3200 μm screens was considered to consist of the large particles (LP) (Dixon and Milligan 1985) whereas proportions of fecal matter retained on the 2500, 1000, 500 and 250 μm screens plus the residues were defined as small particles (SP). The proportions of LP increased linearly (P = 0.02) with increasing weights placed in the rumen.

Geometric means and standard deviations of fecal particle size estimates based on the logarithmic normal distribution are also shown in Table 4.2. Addition of 0, 9 or 18 kg weights to the rumen linearly increased (P = 0.03) the geometric mean size of fecal particles (Table 4.2).

Duration of reticular contractions was directly related to the proportion of LP (r = 0.90, P = 0.002) (Table 4.3). There was also a significant relationship between geometric mean size of fecal particles and duration of reticular contractions (r = 0.61, P = 0.08). The product of amplitude times duration (r = 0.82, P =0.006), and of FxD (r = 0.94, P = 0.0002) of reticular contractions also were directly related to the proportion of LP of fecal matter (Table 4.3). No relationships were apparent between FxA of reticular contractions and any particle size group of fecal matter (Table 4.3). The proportion of fecal LP was also directly related (r = 0.93, P = 0.0002) to FxAxD of reticular contractions (Table 4.3).

4.4 DISCUSSION

4.4.1 Reticular contraction attributes

Since addition of the 18 kg weight to ventral sac of the rumen caused at most a 15% increase in volume of RR contents compared to the 52% increase in the weight of RR contents, the results of this study were discussed only in terms of the weight of the experimental variable. Results of the present study indicated that the addition of weights to the rumen resulted in a quadratic increase in the frequency of reticular contractions. Okine et al. (1989) reported that the addition of 24 kg weights to the rumen reduced the frequency of reticular contractions. Less weight was used in the present study and this could have resulted in less stimulation of epithelial mechanoreceptors and therefore a smaller inhibitory effect on reticular contractions than in the previous study. Also, the polyethylene containers filled with sand which were used in the previous experiment (Okine et al. 1989) were tied with 10 cm lengths of polypropylene twine around the circumference of a semi-flexible plastic hose and thus settled in fixed positions on the floor of the ventral sac. In contrast, the polyethylene containers used in the present study were not tied and were capable of being moved by RR contractions. Individual containers were sometimes found in the cranial and the ventral blind sacs of the rumen. The movements of the weights could have resulted in smaller reflex inhibition arising from less stimulation of the epithelial mechanoreceptors and therefore a less persistent discharge of these receptors. It is the persistent discharge of these receptors which causes the inhibitory effects on reticular contractions (Leek 1987).

In confirmation of earlier results (Okine et al. 1989), there was a linear increase in the duration of reticular contractions with the addition of weights to the rumen. Studies in cattle (Deswysen 1987) showed that the reticulo-omasal orifice is opened to its maximal size for about 10 to 12 seconds starting from the beginning of the second phasic reticular contraction and if the orifice is not masked by the lips of the reticular groove, the increased duration of reticular contraction may result in increased flow of digesta from the RR.

Colvin et al. (1978) reported that the stimulation of tactile receptors of the RR enhanced amplitude of contractions but that different diets have varying effects on these receptors. Change in the amplitudes of reticular contractions reported in this study cannot be explained by diet effects, however, since only one diet was fed. The amplitude of contractions is also influenced by rapidly-adapting mechanoreceptors of the RR. Moderate stimulation of these receptors causes an increase in amplitude, whereas more extensive stimulation causes a decrease (Leek 1969). In our study, the decrease in amplitude of reticular contractions with the addition of weights to the rumen could be due to excessive stimulation of the rapidly-adapting mechanoreceptors. Amplitude of reticular contractions change during the day and have also been associated with changes in feeding activity and the physical form of the diet (Colvin et al. 1978). It has been suggested that changes in amplitude should be accompanied by changes in the passage of digesta from the RR although there is no unequivocal proof for this concept (Ulyatt et al. 1986). The work reported here does not clarify the equivocal nature of amplitude in influencing passage rate constants since the rate constants were not measured and amplitude of reticular contractions in this study was not related to either the proportion of fecal LP or the geometric mean size of fecal matter.

4.4.2 Fecal particle distributions

To determine particle size distribution fecal samples were manually stirred in a rotary fashion as the screened end cylinder was lifted through a large volume of water. Using this procedure the long axis of particles tend to orient parallel to the surface and thereby present their largest dimension to the screen openings. On the other hand, the mechanical sieving techniques used in other studies could lead to a different orientation of particles and could thus give different results (Poppi et al. 1980). Therefore comparisons of particle size distributions obtained by this and other methods should be made with caution as suggested by Dixon and Milligan (1985).

Goodness of fit of the actual weights of fecal particles retained on the various screen sizes to a lognormal distribution were tested using the Kolmogorov-Smirnov one-sample test (Sokal and Rohlf 1981). The results ($P = 0.28$; $P = 0.35$ and $P = 0.28$), for steers with 0, 9, and 18 kg weights in their rumen, respectively, showed that each variable did not deviate significantly from a theoretical lognormal distribution indicating that the fecal mean particle sizes conformed to logarithmic normal distribution (Waldo et al. 1971). The increases in the geometric mean size of fecal particles and in the proportions of fecal particles retained on the 3200 and 2500 μm screens with the addition of weights to the rumen are similar to results obtained by Van Soest (1982) and Faichney (1986) with increasing intake. Faichney (1986) interpreted such results as changes in the distribution of particles within the size range capable of exiting from the RR and cautioned that increases in size of particles appearing in the feces should not be construed to mean that the critical size for passage of particles is changed by increasing intake. This caution seems plausible since the particles retained on the 6800 μm screen constituted only 0.3% of the total fecal material across all treatments. However, Van Soest (1982), Cardoza and Mertens (1986) and Van Soest et al. (1988) contend the limiting particle size for passage from the RR is not a constant but is affected by high feed intakes and the type of feed. There is a need for more refined concepts and data to resolve the controversy.

4.4.3 Relationship between reticular contraction attributes and fecal particles

Sissons et al. (1984) reported positive relationships between frequencies of reticular spike-bursts and movement of digesta from the RR which suggested that increased passage rate constants were related to increased frequencies of contractions. Reid (1963) also reported that there was a positive relationship between the amount of feed consumed and both the extent and persistence of increases in frequency of reticular contractions. The conclusions of Ulyatt et al. (1984) however, suggest that increases in passage rates and passage rate constants are not controlled by changes in the frequency of reticular contractions. Evidence from Bosch et al. (1988), and Okine et al. (1989) and the lack of relationships between frequency of reticular contractions and either fecal particle size distribution or geometric mean sizes of fecal particles in this study, also suggest that changes in fecal particle size distributions are not necessarily due to increases in frequency of reticular contractions. Calculations of fluxes of digesta through the reticulo-omasal orifice based on the assumption of a positive relationship between frequency of reticular spike bursts and movement of digesta from the RR (Sissons et al., 1984), should thus be treated with caution.

The only individual parameter of reticular contractions which showed a positive relationship with changes in distribution of fecal particle sizes and geometric mean sizes was duration of reticular contraction which explained 81% and 38%, respectively, of the variation in the proportion of LP of fecal matter and geometric mean size of fecal particles. Multiple regression equations also showed that duration, and not frequency or amplitude, contributed significantly to the relationships between reticular contraction attributes and fecal particle size distribution. In addition AxD, FxD and FxAxD explained 68%, 88% and 87% of the variation in the proportion of LP in the feces, respectively. These positive relationships between duration, either as an individual parameter, or as a product of amplitude and/or frequency and changes in fecal particle size distribution are interpreted to indicate that the changes in distribution of fecal particle sizes and the increase in geometric mean sizes caused by the addition of weights to the rumen is primarily associated with increases in the duration of reticular contractions rather than either the amplitude or frequency of reticular contractions. This agrees with recently developed concepts

(Okine et al. 1989). The reticulo-omasal orifice opens starting from the beginning of the second biphasic reticular contraction and if the orifice is not masked by the lips of the reticular groove, increases in the duration of contractions by the addition of weights to the rumen, should result in the orifice remaining open for a longer period for RR outflow. When the orifice is open for extended duration, the probability of escape of larger particles is enhanced and the geometric mean size of fecal material would be increased.

4.4.4 Conclusion

In conclusion adding weights in the the ventral sac of the rumen caused significant increases in the proportion of large particles and in the geometric means in fecal matter. The changes in the distribution of particles in the fecal matter and the increase in fecal geometric means were associated with increases in the duration of reticular contractions and not associated with changes in either the frequency or the amplitude of reticular contractions.

4.5 REFERENCES

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Table 4.1. EFFECTS OF ADDING WEIGHTS TO THE RUMEN OF STEERS ON RETICULAR CONTRACTION ATTRIBUTES

Item	Weights in rumen (kg)			SE†	Probability††	
	0	9	18		L	Q
Frequency (min^{-1})	1.4	1.7	1.6	.09	.05	.07
Duration (sec)	5.2	5.5	6.2	.21	.04	.13
Amplitude (mm Hg)	11.3	10.9	10.5	.23	.08	.14
Frequency x Amplitude	15.8	18.5	16.8	.25	.07	.09
Frequency x Duration	7.4	9.3	9.9	.30	.04	.15
Amplitude x Duration	58.7	59.7	65.4	.64	.05	.09
Frequency x Amplitude x Duration	89.0	100.8	105.7	3.15	.06	.10

†= Pooled standard error of the mean (df = 6) with three observations per mean.

††L= Linear effect; Q = Quadratic effect.

Table 4.2. EFFECTS OF WEIGHTS IN THE RUMEN OF STEERS ON THE PROPORTION OF FECAL DRY MATTER WHICH WAS RETAINED ON SCREENS OF VARIOUS SIZES AND PARTICLE SIZE DISTRIBUTION

	Weights (kg) in rumen				Probability††	
Item	0	9	18	SE†	L	Q
Particles retained on screen (proportion of total particles)						
6800 μm	.001	.003	.003	.001	.698	.820
3200 μm	.010	.040	.054	.001	.012	.054
2500 μm	.133	.163	.168	.002	.007	.040
1000 μm	.146	.160	.152	.005	.110	.171
500 μm	.211	.202	.200	.011	.395	.642
250 μm	.254	.201	.201	.019	.177	.358
Residue	.244	.236	.222	.017	.180	.222
Geometric mean particle size						
Log_{10} mean	2.542	2.617	2.687	.011	.026	.200
Log_{10} SD	.423	.472	.473	.005	.026	.077

†- Pooled standard error of the mean (df - 6) with nine observations per mean.

††L - Linear effect; Q - Quadratic effect.

Table 4.3. COEFFICIENTS OF DETERMINATION (R^2), SLOPES AND INTERCEPTS OF LINEAR REGRESSIONS BETWEEN FECAL PARTICLE SIZE DISTRIBUTIONS AND RETICULAR CONTRACTION ATTRIBUTES

Item	Fecal particle distribution	
	Large†	Geometric mean size
Frequency (min^{-1})		
Intercept	.035	2.735
slope	.001	-.036
SE††	.037	.419
R^2	.0001	.001
Probability	.976	.935
Duration (sec)		
Intercept	-.180	1.038
slope	.038	.292
SE††	.007	.142
R^2	.815	.376
Probability	.002	.079
Amplitude (mm Hg)		
Intercept	.287	4.796
slope	.024	-.199
SE††	.016	.194
R^2	.256	.226
Probability	.202	.340
Frequency x Amplitude		
Intercept	-.108	2.833
slope	.009	-.009
SE††	.007	.056
R^2	.224	.004
Probability	.242	.879
Frequency x Duration		
Intercept	-.115	2.297
slope	.017	.044
SE††	.002	.076
R^2	.880	.046
Probability	.0002	.584
Amplitude x Duration		
Intercept	-.281	-.109
slope	.005	.046
SE††	.001	.020
R^2	.676	.420
Probability	.006	.058
Frequency x Amplitude x Duration		
Intercept	-.165	1.816
slope	.002	.009
SE††	.0003	.009
R^2	.871	.129
Probability	.0002	.305

† Fecal particles retained by the 6800 and 3200μm screens.

††SE of slope (n = 9, df = 7).

V. RETICULAR CONTRACTION ATTRIBUTES, EXTENT OF DIGESTION AND PASSAGE OF DIGESTA FROM THE RUMINO-RETICULUM IN CATTLE FED ROUGHAGE DIETS[1]

5.1 INTRODUCTION

Clearance of indigestible residues from the rumino-reticulum (RR) has been reported to be limited by two processes; the rate of physical reduction of digesta particles to sizes capable of exiting the RR, and the rate of passage of particles from the RR (Poppi et al., 1980; Ulyatt et al., 1986). However, there is no conclusive evidence in the literature as to which of these two processes is the main rate-limiting step in clearing the RR (Ulyatt et al., 1986). While there are reports suggesting that there is a threshold particle size above which most material fail to leave the RR (Reid et al., 1977; Poppi et al., 1980), there are also reports of highly significant increases in mean size of fecal particles with increases in feed intakes (Van Soest, 1982, Van Soest et al. 1988). In addition 60 to 70% of the particulate matter present in the RR is normally below the apparent critical particle size for passage (Ulyatt et al., 1986; Reid et al., 1977; Weston, 1989). This suggests that the major rate-limiting step in clearing feed residues from the RR may be the regulation of passage and not particle size reduction.

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[1] A version of this chapter has been submitted for publication. Okine, E.K. and G.W. Mathison. 1990. J. Anim. Sci.

The physiology of the regulation of both particulate and liquid passage from the RR is poorly understood (Ulyatt et. al., 1986). The general belief of a positive relationship between frequency of reticular contraction and passage rate of liquid digesta from the RR (Reid, 1963; Sissons et al., 1984) has been questioned by Okine et al. (1989). Data from rumen contractions (Bosch et al., 1988), reticular contractions (Okine et al., 1989), and both reticular and rumen contractions Ulyatt et al. (1984), show that passage of both liquid and particulate digesta from the RR may not be controlled by changes in frequency of contractions. In addition Okine et al. (1989) have shown that changes in particulate fractional passage and fluid dilution rates appear to be related more to the duration than to the frequency of reticular contractions. There is thus a need for further information of the relationship between attributes of reticular contractions and passage of digesta from the RR, since such information is central to understanding the factors controlling the voluntary intake and digestion of roughages by ruminant animals.

The primary objective of this study was to determine if changes in attributes of reticular contractions (frequency, duration and amplitude) are primarily responsible for changes in passage of digesta from the RR in cattle fed a forage-based diet. Changes in extent and rate of digestion in the RR, and extent of digestion in the duodenum, and feces were also measured.

5.2 MATERIALS AND METHODS

5.2.1 Animals and feed

Four non-lactating Holstein dairy cows (mean liveweight 692 kg) were used in a 4 x 4 latin square designed experiment. Each period consisted of 33 d during which cows were fed a diet of consisting of a 40:40:20; mixture of bromegrass (Bromus inermis), timothy (Phleum pratense) and alfalfa (Medicago sativa) hay (Table 5.1), ground to approximately 6 cm through a tub grinder[2]. The animals were fed at maintenance (M), 1.3M, 1.5M and 1.7M. The cows were allowed 14 d to adapt to each feeding level before measurements were begun. Rations were offered in equal proportions twice daily at 0900 and 1600. Trace mineralized salt licks[3] and water were available free-choice. At least 180 d before being used for the experiment the cows were each fitted with a 10-cm (i.d) soft rumen cannula (Bar Diamond Inc., Parma Idaho) and a T-type duodenal cannula (Robinson et al., 1985) in the proximal duodenum 3-5 cm distal to the pylorus. The duodenal cannulas utilized in this experiment were designed to ensure accurate representation of digesta actually passing the sampling site by causing total digesta diversion through the cannula (Robinson et al., 1985). Cows were maintained indoors in individual pens with continuous lighting at an ambient temperature of 20-22°C throughout the experiment.

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[2] Model 390, Sperry New Holland, Pennsylvania.
[3] Composition:>99% NaCl, .004% Co, .007 I.

5.2.2 Estimation of rumino-reticulum pool sizes

Rumino-reticulum digesta was manually evacuated on 4 consecutive days; at 1000 h (day 28), 0600 h (day 29), 2400 h (day 30) and 1400 h (day 31) during each period using the procedures outlined by Robinson et al. (1987). Rumino-reticulum dry matter (DM), acid detergent fiber (ADF), neutral detergent fiber (NDF) contents and pool sizes were calculated from the contents of rumen digesta and analyses of samples collected during the four evacuations.

5.2.3 Passage Rates

Movement of particulate material was determined using NDF pool sizes estimated from RR evacuations and by the use of chromium (Cr) mordanted to the NDF of the hay. The hay was first washed in a laundry machine with water at 95°C containing a commercial detergent using three water rinses. The residue was then soaked over-night in acetone, rinsed till the water became clear and dried at 65°C for 48 h. This material was then mordanted with Cr according to the method of Uden et al. (1980). Particles contained 3.5% Cr after mordanting.

At 0900 h on d 9 of each period, the cows were prime-dosed intraruminally with Cr-mordanted fiber containing 1 g Cr. From 1600 h on d 10 till 1600 on d 18, Cr-mordanted fiber containing .71 g Cr was dosed to the rumen at 4-h intervals. Duodenal samples for particulate outflow determinations were collected every 3 h starting at 0900 h on d 15 till 0900 h on d 18. Total digestive tract passage rate constants were determined from the decline of Cr concentration in fecal samples collected every 6 h for 72 h after termination of the RR administration on d 18. Samples were frozen till analyzed.

Fractional passage rates by evacuation (Kpe) and passage through the whole digestive tract (Kpt) were calculated using the following procedures: Kpe = duodenal flow of NDF/rumen NDF pool size; Kpt = first-order rate-constants estimated by the fecal decline of Cr concentration in samples collected every 6 h for 72 h following the termination of ruminal administration of Cr. Rates of digestion (Kd) of the total NDF pool were calculated from the following relationship: daily NDF intake/rumen NDF pool = Kpe + Kd.

Rumen fluid or non-DM dilution rates were estimated twice in each period using cobaltethylenediamine tetra-acetic acid (CoEDTA). On d 14 and d 19 of each period, the cows were dosed intraruminally at 0600 h with CoEDTA containing 5 g of Co prepared according to the procedures of Uden et al. (1980). Rumino-reticular fluid for fluid dilution rate estimations was collected from the reticulum, and the dorsal, ventral and caudal sacs of the rumen using a disposable syringe with attached strainer at the end at 0.5, 1 h and then hourly until 15 h post-dosing. Samples for fluid dilution rate studies were thoroughly mixed, subsampled and frozen for subsequent analyses.

5.2.4 Reticular Motility

On d 20, 22, 24, and 26 of each period, the frequency, duration and the amplitude (index of force) of reticular contractions were measured following the procedures of Okine et al. (1989). Briefly, a fluid-filled open-tipped catheter (polyvinylchloride, .09 mm i.d.) was inserted into the reticulum and connected to a pressure transducer[4] and a Beckman physiological recorder[5]. Weights (40 g) were fixed 15.0 cm from the anterior portion of the catheter to ensure that the catheter remained in the reticulum. Pressure transducers were maintained at a height that was level with the tip of the catheter. Water (2.5 ml/min) was infused into the catheter using a continuous infusion pump[6] to prevent RR digesta from entering the catheter. Motility recordings were made over four 6 h measurement periods in the morning (0600 to 1200 h), afternoon (1200 to 1800 h), evening (1800 to 2400 h), and dawn (2400 to 0600 h), respectively. Measurements of reticular contraction attributes on two cows chosen at random were recorded for 6 h in the morning and evening, respectively, while the other two cows were recorded in the afternoon and at dawn on d 20. On d 22, the schedule was crossed-over. Days 24 and 26 were repeats of d 20 and d 22, respectively. This arrangement ensured that by d 26, all four cows had undergone a repeated complete 24 h cycle of recordings of frequency, duration and amplitude of reticular contractions. The 24 h cycle could then be divided into periods of eating, ruminating and resting. The odd days were designated days of rest, since the animals were not allowed to lie down during the measuring periods to ensure an accurate measurement of amplitudes of reticular contraction.

The opening of the reticulo-omasal orifice was assumed to be equal to the number of reticular contractions (Freer et. al, 1962; Wyburn, 1980; Deswysen and Ellis, 1989). The daily number of reticular contractions per unit weight of digesta transferred through the reticulo-omasal orifice was calculated as an expression of the efficiency of digesta transfer (Deswysen and Ellis, 1989). Similar expressions of efficiency of digesta transfer were calculated for total duration and total amplitude of reticular contractions.

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[4] Model P23DB, Gould Statham, CA.
[5] Model R-612, Electronic Division, IL.
[6] Model MP-13G54, SA. Zurich.

5.2.5 Apparent Digestibility

Dorsal, ventral, reticular, duodenal and fecal samples collected at 3 h intervals starting at 0600 on d 15 till d 18 of each period were used for apparent digestibility determinations. The samples collected at 3 h intervals were bulked across days, subsampled and analyzed for DM, CP, OM, NDF, ADF and acid detergent lignin (ADL). Apparent nutrient digestibility coefficients were estimated by the marker ratio technique using ADL as an internal marker (Merchen, 1988).

5.2.6 Chemical analyses

Dry matter was determined by drying at 110°C in a forced-air oven to a constant weight. Crude protein was determined by the Kjeldahl method for nitrogen according to AOAC (1980) using method 2.057. Organic matter was determined by ashing a dried sample at 550°C (AOAC 1980, method 2.176). Neutral detergent fiber, ADF and ADL were determined using the methods described by Van Soest and Robertson (1980). Cellulose and hemicellulose concentrations were estimated by subtraction of ADL from ADF and ADF from NDF.

Chromium in duodenal and fecal samples was analyzed according to the procedure described by Okine et al. (1989). Briefly, 50 g samples were oven-dried at 65°C for 3 d and then ground through a Wiley mill fitted with a 1 mm screen. Approximately 500 mg of the ground material was digested in 30 ml of 4 M-nitric acid at room temperature for 4 h and then for 12 h at 75°C. The digested solution was centrifuged (1000 g for 10 min) to obtain the supernantant fraction which was analyzed for Cr content on an atomic absorption spectrophotometer[7] using standard atomic absorption conditions for Cr determination. Chromium concentration in samples was calculated with reference to the weight of sample, DM of sample, volume of solution, density of nitric acid and dilution factors (Robinson et al., 1986).

Prior to analyses, a subsample of rumen fluid was thawed, filtered through Whatman 54 filter paper (Whatman International Ltd. Maidstone, England) with the supernantant fraction being analyzed for Co after a suitable dilution with 0.1 M-hydrochloric acid using the atomic absorption spectrophotometer. The dilution rate-constants for ruminal non-DM content were also calculated as first-order rate-constants with a correction for the basal amount of Co present in the RR.

5.2.7 Statistical Analyses

The data were analyzed as a 4 x 4 latin square design. Analyses of variance for main effects only were computed using the SPSSX (SPSSX, Inc., Chicago, USA) ANOVA program, with six degrees of freedom (df) in the error term, and feed intake levels (df - 3), animals (df - 3), and periods (df - 3) as main sources of variation. Linear and quadratic effects of equal spacing in treatment levels on dependent variables were computed using the one-way procedure in SPSSX. Relationships between the data for the eating, ruminating and resting phases of each feeding cycle were computed using simple and all-possible multiple regressions, with coefficients of determinations (R^2) and standard errors of estimate being calculated according to procedures outlined by Steel and Torrie (1980).

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[7] Model 4000; Perkin Elmer Corp., Norwalk, Conn. 06856, USA.

5.3 RESULTS

5.3.1 Feed Composition and Intake

Chemical composition of the diet is as shown in Table 5.1. While there was little variation in the various batches of feed the determined compositions of each batch for each period were used for the calculation of intake of dietary components. The average DM intakes by the cows were 11, 14.3, 16.5 to 18.7 kg.d^{-1} representing maintenance (M), 1.3M, 1.5M and 1.7M feeding levels, respectively, (Table 5.2).

5.3.2 Apparent Digestibilities

Extent of digestion of DM, OM, NDF, ADF, hemicellulose and cellulose decreased linearly in all regions of the rumino-reticulum and the duodenum as feed intake increased from maintenance to 1.7M (Table 5.3). There was a progressive increase in the extent of digestion from the dorsal sac, the ventral sac, the reticulum to the duodenum for NDF with increases of 35.7, 3.3 and 18.2 percentage points from dorsal to ventral, ventral to reticulum and from the reticulum to the duodenum, respectively, (Table 5.3); similar increases were calculated for all components of the diet. For all feed components, at least 76% of the extent of total digestion occurred prior to the duodenum (Table 5.3).

5.3.3 Passage Rate

Rumen NDF and OM pool sizes increased linearly (P = .04 and P = .05, respectively) as feed intake increased (Table 5.4). Level of intake had no effect (P = .66) on the ratio of NDF intake to the rumen

NDF pool size. Fractional passage rate through the entire gastrointestinal tract (Kpt) and rumino-reticulum passage rate constants of NDF based on evacuation data (Kpe) both increased (P = .04 and P = .03, respectively) with increase in intake (Table 5.4). Flow of NDF and OM at the duodenum increased linearly (P = .007 and P = .005, respectively) with increased feeding level. Fractional digestion rates (Kd) decreased (P =.07) with intake (Table 5.4).

Content of non-DM in the rumen and dilution rate of non-DM content both increased linearly (P = .07 and P = .07, respectively) as feed intake increased (Table 5.4). Dilution rates of rumen non-DM content before feeding (P = .08) and during and after feeding (P = .06) increased with increased feed intake. There were increases of 28.8 and 148.6% in the dilution rates before feeding and during and after feeding between the lowest and highest intake levels, respectively (Table 5.4). Dry matter content (P = .005) and total rumen digesta content (P = .08) increased as feed intake increased (Table 5.4).

5.3.4 Motility Studies

Frequencies of reticular contraction during the eating, ruminating and resting phases of the feeding cycle were not affected (P = .09; P = .07; P = .09 respectively) by feeding level (Table 5.5). However, within each feeding level, frequency of contraction was lowest during the resting phase, intermediate during the ruminating phase and highest during the eating phase (Table 5.5). Duration of reticular contractions increased linearly during eating, ruminating and resting, (P = .03; P = .01; P = .04, respectively), as feed intake level increased, (Table 5.5). Within each feeding level, duration of contraction was always highest during resting compared to duration of contraction during eating and ruminating. Increase in feed intake level also resulted in linear increases in amplitude of reticular contractions during eating (P = .01), ruminating (P = .02) and resting (P = .02) (Table 5.5). The product of amplitude and duration of reticular contractions (AxD) which could determine the amount of work done per contraction increased linearly during eating (P = .04), ruminating (P = .04), and resting (P = .03) as feed intake increased (Table 5.5).

5.3.5 Time Spent Eating, Ruminating and Resting

Time spent eating (P = .006), ruminating (P = .009), and total time spent eating and ruminating (P = .004) increased while time spent during the resting phase of the feeding cycle decreased (P = .002) as DM intake increased from maintenance to 1.7M (Table 5.6). Within each feeding level, more time was spent resting compared to time spent ruminating and time spent eating. However, as a percentage of the total time spent eating, ruminating and resting, time spent resting decreased from 68.3% at maintenance to 42.2% at 1.7M (Table 5.6).

5.3.6 Relationships between Intake, Eating and Ruminating Time, Reticular Contraction Attributes and Passage Rates

Time spent eating, ruminating and total time spent eating and ruminating all showed positive relationships with fractional passage rates and duodenal NDF flow. However, the variations in both fractional passage rate of NDF and duodenal NDF flow explained by the time spent eating, ruminating and total time spent eating and ruminating were all not significant (Table 5.7).

Dry matter intake was positively correlated with frequency ($r = .86$, $P = .0001$), duration ($r = .90$, $P = .0001$) and amplitude ($r = .85$, $P = .0001$) of contractions. Duodenal flow was also positively correlated ($r = .90$, $P = .0001$) with DM intake. Duodenal NDF flow was positively related to frequency ($r = .88$, $P = .0001$), duration ($r = .98$, $P = .0001$) and amplitude ($r = .96$, $P = .0001$) of contraction and AxD ($r = .98$, $P = .0001$) (Table 5.8). Although the total daily number of reticular contractions increased with increase in intake, the number of contractions per kg of duodenal NDF flow decreased linearly ($P = .0001$) from 600 at maintenance to 425 at the 1.7M feeding level (Figure 5.1). In contrast, total duration ($P = .0001$), total amplitude ($P = .0001$) (Figures 5.2, and 5.3) and total AxD ($P = .0001$) per kg of duodenal NDF flow increased with increased DM intake.

All-possible multiple regression equations depicting the interrelationship of frequency, duration, amplitude and AxD and duodenal NDF flow are as shown in Table 5.9. The coefficient of determination ($R^2 = .97$) did not change for all-possible combinations of reticular contraction attributes which were factored into the regression equations. However, the variations in duodenal NDF flow explained by each attribute over and above the other attributes differed (Table 5.9). The variation in duodenal NDF flow explained by frequency of reticular contraction ($P = .76$) was not significant when compared to the variation explained by duration ($P = .0001$) amplitude ($P = .0001$) and AxD ($P = .0001$). Duration of contraction ($P = .002$) and AxD ($P = .001$) were significant in explaining the variation in duodenal NDF flow compared to amplitude. Duration ($P = .486$) and

AxD (P = .117) both did not explain any more variation in duodenal NDF flow over and above the other. When all the individual attributes of reticular motility were factored into the equation, duration of contraction (P = .0514) was more significant in explaining the variation in duodenal NDF flow compared to frequency (P = .7122) and amplitude (P = .2265). Frequency, amplitude, duration and AxD did not explain a significant portion of the variation in duodenal NDF flow over and above the other when all of them were factored into the regression equation (Table 5.9).

5.4 DISCUSSION

5.4.1 Feed Intake, Extent of Digestion and Digestion Rates

The decrease in the extent of digestion in the total gastrointestinal tract of all feed components as intake level increased is in agreement with results from cattle fed a mixed diet (Staples et al., 1984), but in contrast to observations made on sheep fed at a high and low intake (Ulyatt et al., 1984). In agreement with results of Robinson et al. (1987) a variable proportion of the depression in digestibility of NDF in this study can be attributed to ruminal effects since there was a 4.7% decrease in kd and a 21% increase in Kpe when feed intake was increased from maintenance to 1.7M. In contrast, in the study of Ulyatt et al. (1984) there were increases of 3.2% and 30.4% in Kp and Kd of fiber, respectively, with increased intake and the effects of Kp and Kd on digestibility may have cancelled out.

Within the rumino-reticulum, the ventral sac had the greatest depression in the extent of digestion which was calculated as the difference in digestibilities at 1.7M and at M, with values of 17.4, 17.2, 6.8 and 18.1% for NDF, ADF, hemicellulose and cellulose, respectively. Corresponding values of 11.6, 9%; 10.2, 7.5%; 5.3, 5.9%; and 7.7, 9.7% were obtained for the same cell wall components in the reticulum and dorsal sac, respectively. The ventral sac is the site where most digestion occurs in the rumino-reticulum, and may be the site most sensitive to changes in Kp and in Kd. Hemicellulose was the cell wall component least digested in the rumino-reticulum with means of 15, 24 and 31% digestion in the dorsal, ventral and reticulum, respectively. These low digestibilities could have been due to the presence of a ligno-hemicellulose complex. Digestion of hemicellulose is inhibited by the presence of lignin (Tanner and Morrison, 1983). Post-ruminally however, hemicellulose was comparatively digested more than the other cell wall components with an increase of 53.3 percentage points in the duodenum over the extent of digestion in the reticulum. The hydrochloric acid secretion in the abomasum contributes to hemicellulose and ligno-hemicellulose complex breakdown (Deswysen and Ellis, 1988) and hence increases the digestibility of hemicellulose.

5.4.2 Passage Rate

As feed intake increased from maintenance to 1.7M, there were increases of 43, 48 and 53% in DM, NDF and OM contents in rumen ingesta, in agreement with results reported by Robinson et al. (1987) and Ulyatt et al. (1984). Increases in ruminal DM, OM and NDF contents however resulted in only an 9.2% increase in total rumen digesta. This moderate increase in total rumen digesta could be attributed to a physiological adaptation of rumen capacity by which there were higher increases in dilution rate of non-DM (96.9%) than in duodenal NDF (79.3%) and OM (91.9%) flow and in Kpe (21%). The rather high increase in non-DM dilution rate compared to the increase in Kp agrees with results of Robinson et al. (1987). The effect of intake on liquid dilution rate is generally greater than the effect on Kp (Owens and Goetsch, 1986).

The 79.3 and 91.9% increases in duodenal NDF and OM flow when DM intake rose from maintenance to 1.7M was attributed to 48.2 and 52.9% increases in rumen NDF and OM pool sizes and a 21% increase Kpe. This contrasts to reports of Ulyatt et al. (1984) who attributed a 43% increase duodenal OM flow to a 45% increase in rumino-reticulum OM pool size only.

The basis for the rather small decrease of 4.7% in Kd compared with the high increases of 21% in Kpe and 48.2 and 52.9% in rumen NDF and OM pool sizes respectively, remains to be determined. It could involve adaptive interactions between ruminal volatile fatty acid (VFA) concentrations, pH, dilution rate, Kpe, Kd, and rumen pool sizes of NDF and OM at high levels of intake. Ruminal pH and VFA concentrations were not measured in this study. It is accepted that ruminal VFA concentrations increase and pH decreases with increased intake with a consequent decrease in Kd (Staples et al., 1984).

Large decreases in Kd may have been be ameliorated in this study through effects of ruminal dilution rates on VFA concentrations and ruminal pH. Staples et al. (1984) reported that peak VFA concentrations occurred progressively at later times after feeding as intake increased, which correlated positively with decreases in pH. Exhibition of longer times for peak drop of ruminal pH has been attributed to higher dilution rates (Rogers and Davis, 1980). Liquid dilution rates during and after feeding in this study increased by 148.6% as intake increased from maintenance to 1.7M. It seems plausible that such high dilution rates may relate to longer times for the pH to fall and thus lead to a smaller depression in Kd. Approximately 119 and 244 liters of rumen non-DM flowed through the reticulo-omasal orifice daily at maintenance and 1.7M, respectively. However, the concentrations of NDF per liter of the rumen non-DM were 2.4 and 2.1%, respectively. Corresponding concentrations for OM were 3.1 and 2.9%. The lack of a significant drop in substrate availability could have contributed to the rather small depression in Kd. The 48.2% increase in rumen NDF pool size coupled with only a 4.7% decrease in Kd ensured a 41.5% increase in total NDF digestion with increased intake.

As feed intake increased, mean retention times of digesta in the RR decreased from 46.3 to 38.3 h, a decrease of 17.3%. This result agrees with results in cattle fed alfalfa hay (Campling et al., 1961), a mixed diet (Collucci et al., 1982; Staples et al., 1984) or a mixed diet with varying proportions of starch (Robinson et al., 1987). The decrease in RR mean retention time was, however, compensated by the digesta spending 49.1 and 44.3 h in the lower digestive tract as intake increased from maintenance through to 1.7M representing increases of 5.5 and 13.5% of the total tract retention times. These results in agreement with those of Staples et al. (1984), may imply that digestion in the lower digestive tract becomes important with increases in intake. Indeed, as intake increased from M to 1.7M, the percentage of total tract digestion of NDF which occurred in the lower digestive tract increased from 17.8 to 24.1%. These results accord with results by Kennedy and Milligan (1978) and Staples et al. (1984) and show the importance of post-ruminal digestion at high intakes.

5.4.3 Relationships between Reticular Contraction Attributes, Chewing Activities, Water and Duodenal Flow

Chewing during eating and ruminating is thought to mediate outflow from the RR by reduction of particles to sizes less than 1.18 mm (Poppi et al., 1980). Chewing activity was not measured in this study. However, time spent chewing tends to parallel total number of chews (Macleod, 1990) and thus in examining the relationship between time spent chewing and Kpe and duodenal outflow of NDF and OM, time spent eating and ruminating were used as an index of number of chews. The variations in both Kpe of NDF and duodenal NDF flow explained by time spent eating, ruminating and total time spent eating and ruminating all were not significant. The relationship between time spent chewing and ruminating and either fractional passage rate or total outflow is equivocal. Macleod (1990) did not find a consistent influence of chewing activity on fractional passage rate. Weston (1989) has also reported that lambs fed a low quality diet spent 100% longer time eating and 20% longer time ruminating than lambs fed a better quality diet. However, the lambs on the low quality diet had clearance rates about 31-56% of the clearance rates in lambs fed the better quality diet.

Feed intake level did not affect the rate of reticular contraction either during eating, ruminating or resting in agreement with results reported by Ulyatt et al. (1984). This may seem contradictory to results of an earlier communication (Okine et al., 1989) where steers with 24 kg weights added to their rumen recorded 14 and 8% decreases in frequency of reticular contraction during eating and resting. The discrepancy, however, is resolved once it is recognized that adding weights to the rumen caused a 21.3% increase in volume compared to 62.7% increase in weight of rumen contents (Okine et al., 1990), and that extreme stimulation of the epithelial mechanoreceptors due to the added weight could have led to a persistent discharge of the epithelial mechanoreceptors resulting in greater inhibitory effects on reticular contractions (Leek, 1987). It is generally recognized that high feed intake, which gives rise to an increased weight of digesta in the rumen, must necessarily lead to increased volume of rumen digesta (Tulloh and Hughes, 1965; Tulloh, 1966) and the effects of parallel increases in weight and volume of rumen digesta on rate of reticular contractions may be different from the effect due to only added weight in the rumen. Within each feed intake level however, frequency of reticular contraction was highest during eating, intermediate during ruminating and lowest during resting in agreement with results obtained by Ulyatt et al. (1984), Grovum (1986) and Okine et al. (1989).

Despite the lack of effect of increased DM intake on rate of reticular contractions during each feeding activity, DM intake still explained 74% of the variation in mean frequency of reticular contractions. This agrees with results of Reid (1963) who reported that for a given animal and feed, there was a positive relationship between amount consumed and both the extent and persistence of increases in frequency of reticular contractions. Dry matter intake also explained 80, 72 and 77% of the variation in duration, amplitude and AxD, respectively. The relationship between frequency of contractions and duodenal NDF flow, however, was more complex. A positive relationship existed between frequency of contractions and flow of duodenal NDF with frequency of contractions explaining 77% of the variation in duodenal NDF flow. However, the 79.3% increase in duodenal flow when intake increased from maintenance to 1.7M resulted in only a 11.9% increase in frequency of reticular contractions.

The disparity between the increases in duodenal flow and frequency of reticular contractions was resolved by calculating the number of contractions needed to transfer 1 kg of NDF from the rumino-reticulum. The calculation was based on the assumption that active outflow occurs during the second phase of the reticular contraction (Balch et al., 1951; Freer et al., 1962; Bost, 1970; Wyburn, 1980). As intake increased, the number of reticular contractions needed to transfer 1 kg of NDF decreased from 598 at maintenance to only 432 at the highest intake. Increased duodenal NDF flow at high intakes cannot therefore be attributed to increases in the number of contractions. These results parallel the smaller number of fluxes required to transfer 1 g of DM or NDF with increased intake (Deswysen and Ellis, 1988). In confirmation with the conclusion of Deswysen and Ellis (1988), the results obtained in this study were interpreted to mean that the efficiency of digesta flux through the reticulo-omasal orifice per contraction increased at high intakes. The basis of the increased efficiency can be attributed to physiological processes within each animal which may override the constraints which prevent digesta from leaving the RR. Such physiological processes could include duration, amplitude and AxD of reticular contractions, effects associated with residual potentially digestible NDF (Deswysen and Ellis, 1988), changes in the composition of the digesta (Malbert and Baumont, 1989) and/or changes in ruminoreticular DM and the rate of transfer of particles from a large particle pool into a small particle pool eligible for exit from the rumino-reticulum.

In confirmation of previous reports (Okine et al., 1989; Okine et al., 1990), there was an increase in the duration of each contraction with increases in DM intake. The increase of 79.3% in duodenal outflow when intake increased from maintenance to 1.7M was positively correlated with a 36.7% increase in duration of reticular contractions. Duration was the attribute of reticular contraction which was significant in explaining the most variation in duodenal NDF outflow when duration and frequency of reticular contractions were factored into an all-possible multiple regression equation. In addition, as intake increased, the time taken to transfer 1 kg of NDF increased from 50.2 min at maintenance to 58.4 min at 1.7M in contrast to the number of contractions which decreased. It appears that as feed intake increases, the decrease in the number of contractions per Kg is compensated for by an increase in the duration of those contractions. Deswysen (1987) reported that the reticulo-omasal orifice is opened to its maximum size for about 10-12 seconds starting from the beginning of the second phase of a reticular contraction and is progressively closed over a total period of 15 to 25 sec. If the other determinants of passage are met such that the reticulo-omasal orifice is not masked by the lips of the reticular groove, there is a motive force to transfer the digesta, and there is a receptive space in the omasum (Ulyatt et al., 1984), the increased duration of contraction may result in increased flow of digesta from the rumino-reticulum.

The other attribute of reticular contraction determining passage is the amplitude of contraction. It is generally accepted that changes in amplitude should be accompanied by changes in outflow of digesta from the rumino-reticulum, since there are pressure differentials between the reticulum and omasum during reticular contraction which could force digesta to the omasum (Balch et al., 1951; Bueno and Ruckebusch, 1974; Ulyatt et al., 1984). However, till now there has not been unequivocal proof for this concept (Ulyatt et al., 1986). Amplitude of each contraction increased by 31.6, 28.3, and 44.2% during eating, ruminating, and during resting, respectively, when intake increased from maintenance to 1.7M. Increase in feed intake also resulted in a 35.3% increase in amplitude per contraction which was positively related to the 79.3% increase in duodenal NDF outflow. Amplitude of reticular contraction was also more significant in explaining the variation in duodenal outflow compared with frequency of contractions when both were fitted into the multiple regression equation. It therefore appears that as feed intake increases, the decrease in the number of contractions is also compensated for by an increase in the amplitude of those contractions resulting in greater outflow.

The variation in duodenal NDF flow explained by AxD was also more significant than that explained by frequency of reticular contractions. Neither duration nor AxD could explain a significant variation in duodenal outflow over and above each other although both were more significant than amplitude of reticular contractions. When all three individual attributes of reticular contractions were factored into the all-possible regression equation, the variation of duodenal NDF flow explained by duration of reticular contraction was more significant than the variation explained by frequency and amplitude. However, when AxD was factored into the equation in addition to the other three attributes of reticular contractions, none of them could explain a significant variation in duodenal flow over and above the other.

5.4.4 Conclusion

In conclusion, this study showed that although frequency, duration and amplitude of reticular contractions each played a role in the regulation of passage from the RR, there was a variation in the contribution from each attribute. On an individual basis, the regulation of digesta passage from the RR was not determined to a significant degree by changes in frequency of reticular contractions. Changes in duration, amplitude and the work done during each reticular contraction were all more important determinants of passage from the RR than frequency. It was also determined that if the requirements for passage such as the reticulo-omasal orifice being opened and not masked by the lips of the reticular groove are met and if there is sufficient force to transfer digesta to the omasum, the duration of contraction may be the most important determinant of passage from the RR.

5.4.5 Implications

Results have important implications in ruminant nutrition and production since they may ultimately lead to ways of improving the productivity of ruminant animals by manipulating the ruminant animal to increase or decrease passage of digesta from the rumino-reticulum and thus influence voluntary intake and digestibility of forage.

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Table 5.1. CHEMICAL COMPOSITION OF THE BROMEGRASS (*Bromus inermis*), TIMOTHY (*Phleum pratense*) AND ALFALFA (*Medicago sativa*) HAY DIET FED TO COWS AT FOUR LEVELS OF INTAKE

Item	Value[a]	SD
Dry matter (%)	93.1	.06
Chemical composition, % DM basis		
Organic matter	90.9	.23
Crude protein	11.2	.04
Neutral detergent fiber	63.4	.12
Acid detergent fiber	39.4	.06
Acid detergent lignin	6.5	.004
Hemicellulose	24.0	.18
Cellulose	32.9	.06

[a] Four observations per mean.

Table 5.2. CONSUMPTION PATTERNS FOR DRY MATTER, ORGANIC MATTER, CRUDE PROTEIN AND CELL WALL COMPONENTS OF DIET FED TO COWS AT FOUR INTAKE LEVELS

Item	Level of intake				
	M[a]	1.3M	1.5M	1.7M	SE[b]
Intake, $kg.d^{-1}$					
Dry matter	11.0	14.3	16.5	18.7	.08
Organic matter	10.0	13.2	15.3	17.1	.10
Crude protein	1.2	1.6	1.9	2.1	.007
Neutral detergent fiber	7.0	8.7	10.1	11.3	.09
Acid detergent fiber	4.3	5.6	4.5	7.4	.07
Hemicellulose	2.6	3.5	3.8	4.5	.09
Cellulose	3.6	4.7	5.8	6.3	.11

[a] Maintenance feeding level.

[b] Pooled SE (6 df) with four observations per mean.

Table 5.3. EXTENT OF DIGESTION FOR DRY MATTER AND CELL WALL COMPONENTS IN VARIOUS SECTIONS OF THE RUMINO-RETICULUM AND AT THE DUODENUM OF COWS FED AT FOUR INTAKE LEVELS

	Level of intake					Probability[c]	
Item	M[a]	1.3M	1.5M	1.7M	SE[b]	L	Q
Total tract extent of digestion (%)							
Dry matter	70.5	68.0	65.0	60.2	1.7	.01	.24
Organic matter	76.4	73.7	71.6	66.7	2.1	.01	.18
Neutral detergent fiber	75.4	72.9	69.7	68.8	2.3	.03	.11
Acid detergent fiber	63.5	61.0	57.9	52.0	1.9	.05	.17
Hemicellulose	49.2	45.8	46.1	42.7	3.1	.06	.10
Cellulose	71.3	70.1	68.8	62.7	1.8	.04	.13
Cumulative % of total tract digestion							
Dorsal sac							
Dry matter	41.2	34.3	30.5	28.0	1.4	.01	.09
Organic matter	42.2	35.3	32.2	29.7	1.7	.04	.11
Neutral detergent fiber	27.9	23.2	20.6	18.9	2.8	.05	.10
Acid detergent fiber	25.5	21.6	19.6	18.0	2.1	.06	.11
Hemicellulose	18.4	15.4	13.6	12.5	1.2	.06	.08
Cellulose	29.8	24.6	22.0	20.1	1.2	.005	.01
Ventral sac							
Dry matter	75.0	66.5	58.7	54.5	3.1	.03	.12
Organic matter	81.9	73.7	66.4	61.6	2.9	.04	.09
Neutral detergent fiber	68.1	60.9	54.7	50.7	2.2	.03	.05
Acid detergent fiber	66.4	59.4	53.0	49.2	2.0	.05	.07
Hemicellulose	27.3	24.7	22.2	20.5	1.3	.01	.15
Cellulose	69.5	62.1	55.6	51.4	2.5	.04	.09
Reticulum							
Dry matter	84.8	74.7	65.7	70.3	1.1	.01	.11
Organic matter	85.4	73.2	66.4	72.3	2.1	.02	.10
Neutral detergent fiber	70.5	62.6	54.7	58.9	2.0	.04	.07
Acid detergent fiber	68.2	60.8	53.0	58.0	1.9	.04	.06
Hemicellulose	34.7	31.7	27.8	29.4	1.4	.01	.13
Cellulose	71.1	69.1	65.9	63.4	2.9	.01	.03
Duodenum							
Dry matter	90.2	89.6	85.0	84.0	1.0	.04	.07
Organic matter	92.5	90.9	87.5	85.6	1.9	.05	.09
Neutral detergent fiber	82.2	81.4	79.9	75.9	.9	.03	.08
Acid detergent fiber	84.4	82.3	79.8	78.5	.4	.001	.04
Hemicellulose	94.0	86.1	81.6	75.6	3.1	.03	.05
Cellulose	90.7	88.9	85.5	82.5	1.2	.05	.09

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[a] Maintenance feeding level.

[b] Pooled SE (6 df) with four observations per mean.

[c] L = Linear effect; Q = Quadratic effect.

Table 5.4. KINETICS OF NEUTRAL DETERGENT FIBER (NDF), ORGANIC MATTER (OM) AND NON-DRY MATTER IN THE RUMINO-RETICULUM, AT THE DUODENUM AND THROUGH THE TOTAL DIGESTIVE TRACT OF COWS FED AT FOUR INTAKE LEVELS

	Level of intake					Probability[c]	
Item	M[a]	1.3M	1.5M	1.7M	SE[b]	L	Q
Intake kg.d^{-1}							
NDF	7.0	8.7	10.1	11.3	.08		
OM	10.0	13.2	15.3	17.1	.10		
Rumen contents, kg							
DM	10.5	12.9	14.5	15.0	.68	.005	.29
NDF	5.6	6.4	7.4	8.3	.23	.04	.62
OM	7.0	8.1	9.4	10.7	.32	.05	.54
Non-DM[d]	77.3	80.7	79.1	80.6	1.89	.07	.12
Total digesta	87.8	93.6	93.6	95.9	3.70	.08	.19
NDF turnover[e], %.d^{-1}							
Passage rate (Kpe)	51.8	54.7	55.4	62.7	2.94	.03	.43
Passage rate (Kpt)	48.9	49.6	50.7	54.2	1.52	.04	.22
Digestion rate (Kd)	73.2	73.4	71.6	69.8	1.27	.07	.14
Non-DM turnover, %.h^{-1}							
Before feeding	5.9	6.2	7.8	7.6	.12	.08	.09
During and after feeding	7.0	10.9	16.9	17.4	.19	.06	.23
Total	6.4	8.3	12.6	12.6	.15	.07	.09
Outflow, kg.d^{-1}							
Duodenal NDF	2.9	3.5	4.1	5.2	.32	.007	.31
Duodenal OM	3.7	5.1	6.7	7.1	.45	.005	.41

[a] Maintenance feeding level.

[b] Pooled SE (6 df) with four observations per mean.

[c] L = Linear effect; Q = Quadratic effect.

[d] Total weight - DM content of digesta obtained by evacuation.

[e] See text for definitions and calculations of turnover rates.

Table 5.5. CHANGES IN RETICULAR CONTRACTION ATTRIBUTES DURING EATING, RUMINATING AND RESTING PHASES OF THE FEEDING CYCLE IN COWS FED AT FOUR LEVELS OF INTAKE

	Level of intake					Probability[c]	
Contraction	M[a]	1.3M	1.5M	1.7M	SE[b]	L	Q
Frequency, min^{-1}							
Eating	1.57	1.58	1.56	1.62	.11	.09	.21
Ruminating	1.32	1.42	1.38	1.57	.06	.07	.32
Resting	1.15	1.18	1.16	1.35	.04	.09	.96
Duration, Sec							
Eating	4.9	5.6	6.0	6.8	.10	.03	.09
Ruminating	4.8	5.6	6.0	6.4	.09	.01	.15
Resting	5.0	5.8	6.5	7.0	.05	.04	.89
Amplitude, mm Hg							
Eating	6.0	6.5	7.5	7.9	.28	.01	.96
Ruminating	6.7	7.1	8.4	8.6	.37	.02	.34
Resting	7.7	8.8	10.7	11.1	.66	.02	.37
Amplitude x Duration							
Eating	29.4	36.4	45.0	53.7	3.2	.04	.23
Ruminating	32.2	39.8	50.4	55.0	3.5	.04	.31
Resting	38.5	51.0	69.6	77.7	3.9	.03	.39

[a] Maintenance feeding level.

[b] Pooled SE (6 df) with four observations per mean.

[c] L = Linear effect; Q = Quadratic effect.

Table 5.6. EFFECT OF DRY MATTER INTAKE ON THE TIME SPENT DURING EATING, RUMINATING AND RESTING PHASES OF THE FEEDING CYCLE IN COWS FED AT FOUR LEVELS OF INTAKE

Item	Level of intake				SE[b]	Probability[c]	
	M[a]	1.3M	1.5M	1.7M		L	Q
DM intake, kg.d-1	11.0	14.3	16.5	18.7			
Time, min.d⁻							
Eating (E)	186.3	260.8	345.5	398.0	15.7	.006	.56
Ruminating (R)	270.0	371.5	391.3	435.0	14.3	.009	.68
Resting	983.8	807.3	703.3	607.0	15.8	.002	.67
E and R	456.3	632.3	736.8	833.0	12.6	.004	.52

[a] Maintenance feeding level.

[b] Pooled SE (6 df) with four observations per mean.

[c] L - Linear effect; Q - Quadratic effect.

Table 5.7. COEFFICIENT OF DETERMINATION (R^2), SLOPES AND INTERCEPTS OF LINEAR REGRESSIONS BETWEEN TIME SPENT EATING, RUMINATING AND TOTAL TIME SPENT EATING AND RUMINATING (X) AND FRACTIONAL PASSAGE RATES AND DUODENAL FLOW OF NEUTRAL DETERGENT FIBER (NDF) (Y)

Time spent (min^{-1})	Fractional passage rate ($\%d^{-1}$)	Duodenal NDF flow ($kg.d^{-1}$)
Eating		
Intercept	42.9380	.8920
slope	.0444	.0102
SE[a]	.0257	.0098
R^2	.50	.53
Probability	.12	.18
Ruminating		
Intercept	35.0350	-.7977
Slope	.0575	.0128
SE[a]	.0323	.0079
R^2	.55	.44
Probability	.11	.23
Eating and Ruminating		
Intercept	39.0941	.0159
Slope	.0257	.0058
SE[a]	.0117	.0032
R^2	.59	.52
Probability	.09	.24

[a] SE of slope (n -16, df - 14).

Table 5.8. COEFFICIENT OF DETERMINATION (R^2), SLOPES AND INTERCEPTS OF LINEAR REGRESSIONS BETWEEN ATTRIBUTES OF RETICULAR CONTRACTIONS (X) AND DUODENAL FLOW OF NEUTRAL DETERGENT FIBER (NDF) (Y)

Contraction	Duodenal NDF flow ($kg.d^{-1}$)
Frequency, min^{-1}	
Intercept	-5.4919
slope	6.9270
SE[a]	1.0244
R^2	.78
Probability	.0001
Duration, sec	
Intercept	- .3887
Slope	.6624
SE[a]	.2289
R^2	.96
Probability	.0001
Amplitude, mm Hg	
Intercept	-1.1777
Slope	.6220
SE[a]	.0471
R^2	.93
Probability	.0001
Amplitude x Duration	
Intercept	1.4945
slope	.0444
SE[a]	.0021
R^2	.97
probability	.0001

[a] SE of slope (n =16, df = 14).

Table 5.9. COEFFICIENT OF DETERMINATION (R^2), SLOPES AND INTERCEPTS OF ALL-POSSIBLE MULTIPLE REGRESSIONS BETWEEN ATTRIBUTES OF RETICULAR CONTRACTIONS (X) AND DUODENAL FLOW OF NEUTRAL DETERGENT FIBER (Y)

Variables	Intercept[a]	Slope[b]	SE[c]	R^2[d]	Probability[e]
1 Frequency, min^{-1}		- .3050	.9689		.758
and	- .1269			.965	
Duration, sec		.6858	.0826		.0001
2 Frequency, min^{-1}		2.2657	1.7893		.553
and	-3.0327			.954	
Amplitude, mm Hg		.4731	.0644		.0001
3 Frequency, min^{-1}		.5630	.7877		.4874
and	.8831			.969	
Amplitude x Duration		.0416	.0045		.0001
4 Duration, sec		.5049	.1255		.0015
and	- .6479			.967	
Amplitude, mm Hg		.1567	.1202		.2151
5 Duration, sec		.1993	.2778		.4859
and	.1993			.969	
Amplitude x Duration		.0311	.0186		.1170
6 Amplitude, mm Hg		- .1013	.1734		.5690
and	1.9447			.969	
Amplitude x Duration		.0513	.0121		.0010
7 Frequency, min^{-1}		.4166	1.1028		.7122
and	-1.0522			.967	
Duration, sec		.4447	.2056		.0514
and					
Amplitude, mm Hg		.1848	.1449		.2265
8 Frequency, min^{-1}		.3551	.9992		.7284
and	.7436			.970	
Duration, sec		.1269	.3524		.7251
and					
Amplitude x Duration		.0342	.0210		.1299
9 Duration, sec		.1606	.3764		.6773
and	1.1987			.969	
Amplitude, mm Hg		- .0374	.2334		.8753
and					
Amplitude x Duration		.0363	.0374		.3509
10 Frequency, min^{-1}		.3406	1.1142		.7655
and	.8226			.970	
Duration, sec		.1198	.4135		.7274
and					
Amplitude, mm Hg		- .0096	.2593		.7909
and					
Amplitude x Duration		- .0354	.0390		.3835

[a] Common intercept of variables in regression equation.

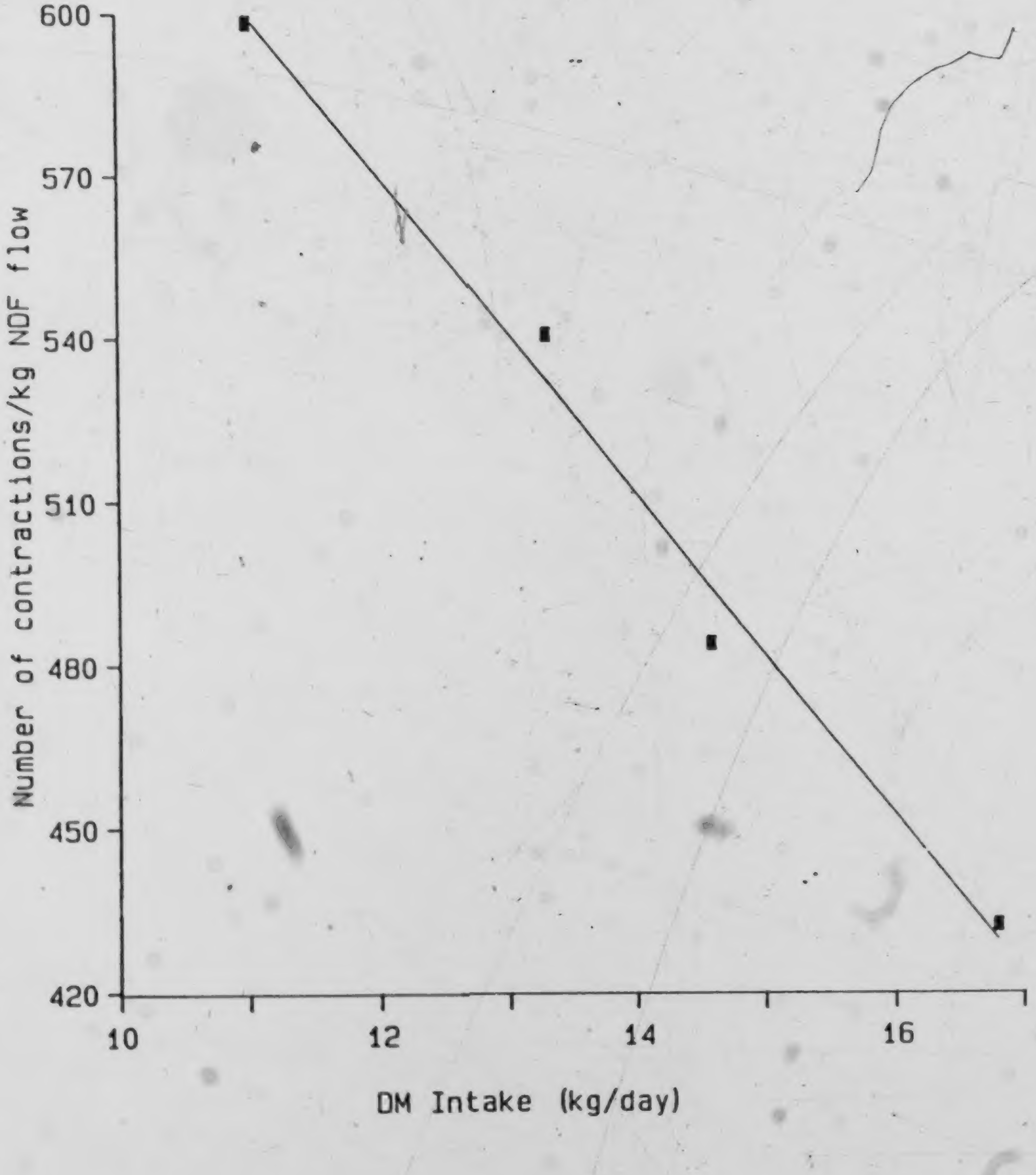
[b] Individual slopes of variables in regression equation.

[c] SE of common slopes (n = 16, df = 14).

[d] Coefficient of determination of variables in regression equation.

[e] Individual probabilities of variables in regression equation.

Figure 5.1. Number of reticular contractions required per kg of duodenal neutral detergent fiber outflow and associated dry matter intake.



600
570
540
510
480
450
420
Number of contractions/kg NDF flow
10
12
14
16
DM Intake (kg/day)

Figure 5.2. Relationship between dry matter intake and time in min associated with 1 kg of duodenal neutral detergent fiber outflow.

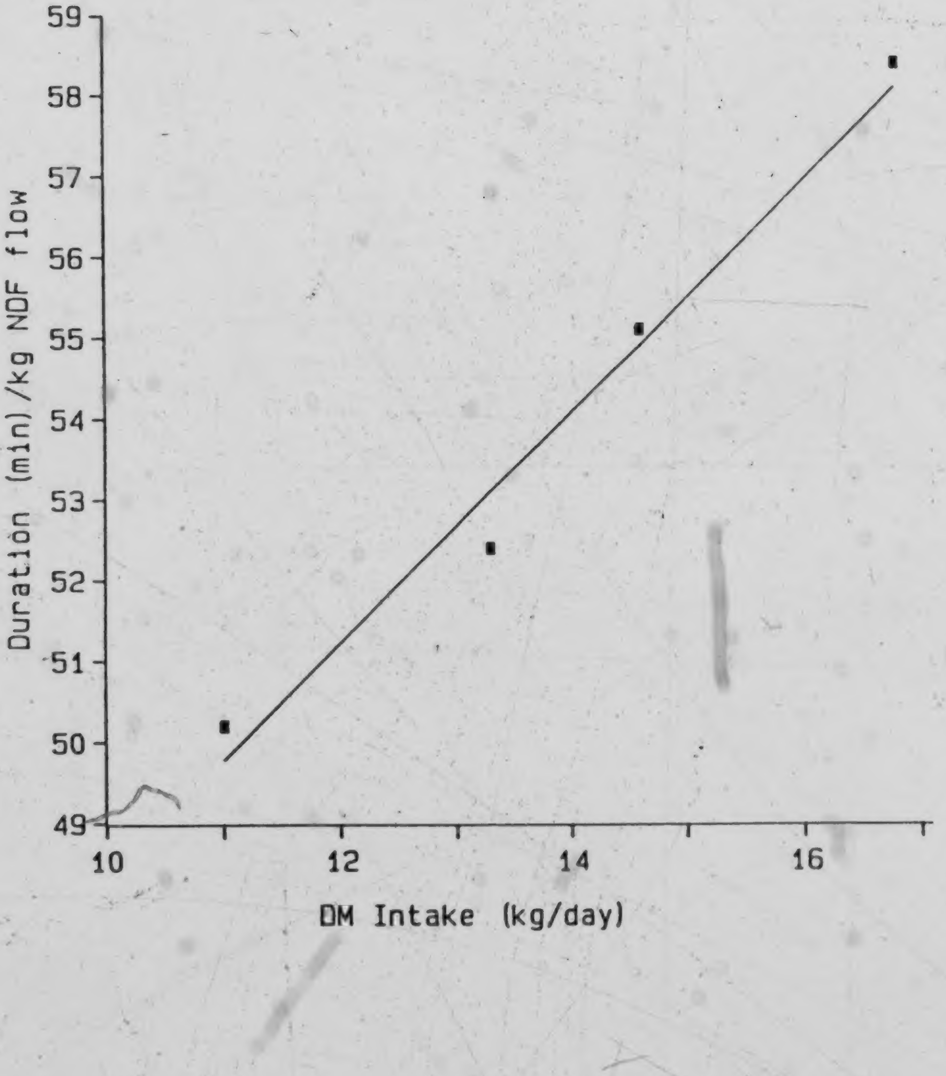
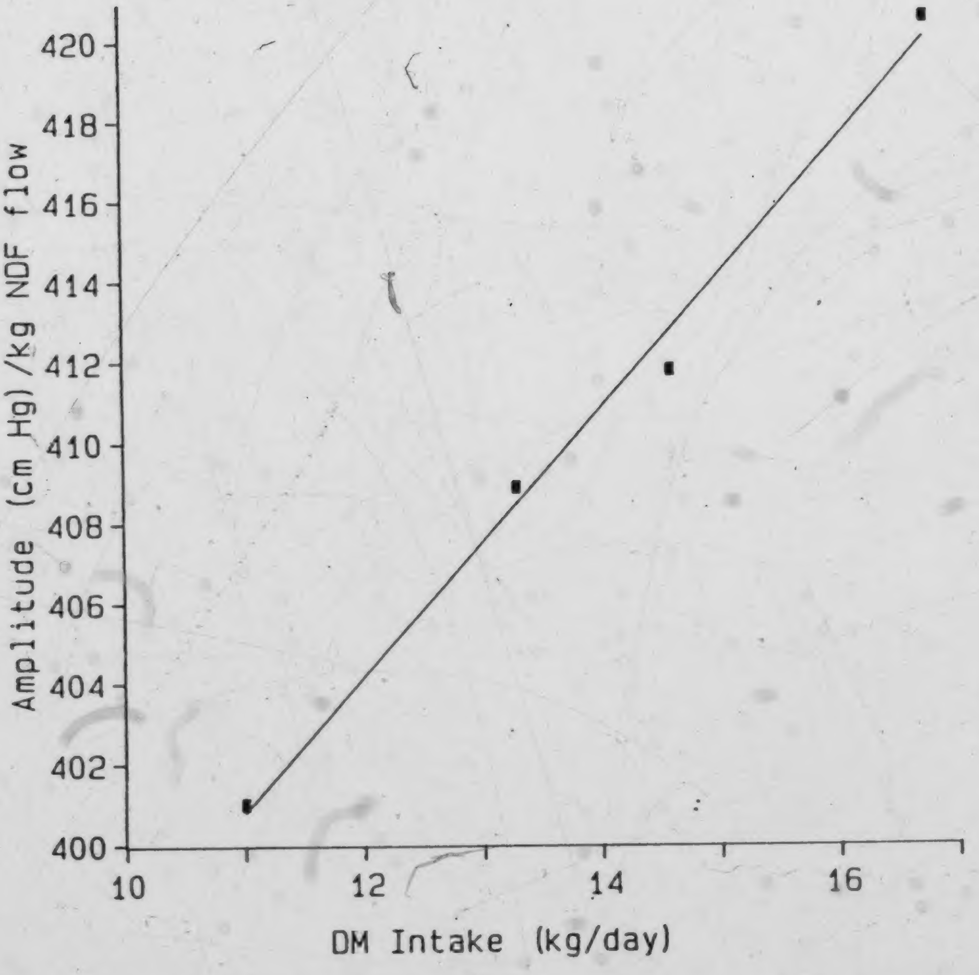

Duration (min)/kg NDF flow
59
58
57
56
55
54
53
52
51
50
49
10
12
14
16
DM Intake (kg/day)

Figure 5.3. Relationship between dry matter intake and the amplitude of reticular contractions associated with 1 kg of duodenal neutral detergent fiber outflow.


Amplitude (cm Hg)/kg NDF flow
420
418
416
414
412
410
408
406
404
402
400
10
12
14
16
DM Intake (kg/day)

VI. GENERAL DISCUSSION AND CONCLUSIONS

Numerous animal factors distinguishing bloat-prone from non-bloating cattle have been documented. These factors include less saliva secretion by bloat-prone cattle (Mendel and Boda, 1961), larger rumino-reticulum (RR) volumes (Cockrem et al., 1983) and higher particulate-matter content in the RR of bloat-prone cattle (Majak et al., 1983), in comparison with non-bloating cattle. The first study (Chapter II) however, provides more evidence on the specific factors which could be responsible for the differences between bloat-prone and non-bloating cattle. One important animal factor contributing to higher amounts of foam produced by bloat-prone cattle was identified in this study. The factor is the dilution rate (DR) of rumen fluid. Although an overall slower DR of rumen fluid has been suggested as a difference between bloat-prone and non-bloating cattle (Majak et al., 1986), our results show that it is more important to consider the relationships between the various components which contribute to the overall DR and foam production. Thus, bloat-prone cattle differ from non-bloating cattle due to a slower DR of rumen fluid during and after feeding with a concomitant higher foam production and not before feeding. It is during and after feeding that animals normally bloat (Howarth, 1975). The results imply that understanding factors involved in controlling passage rates of digesta, especially DR of rumen fluid, will greatly improve efforts aimed at preventing bloat in cattle and could lead to ways of manipulating rumen function.

The 29% decrease in methane production associated with increases of 39 and 30% in passage rate constants for particulate matter and rumen fluid in steers at a constant intake, provided evidence for the first time in the literature of the effect of passage rates on rumen function without confounding effects of feed intake. The results of the second study (chapter III), also provided evidence of a probable shift from a methanogenic fermentation to a propionate fermentation in the rumen due solely to a change in fractional passage rates of particulate matter and rumen fluid and not due to a change in substrates (Fahey and Berger, 1988).

It is known that cattle fed a diet containing a high proportion of a poor quality forage have a greater heat increment of feeding (Kellner, 1926 quoted by Webster, 1980) and greater weight of digesta in their RR than cattle fed concentrate-based diets (Bines and Davey, 1970). However, results from chapter III showed that weight of digesta in the RR is not an important factor influencing the heat production of ruminants.

Although changes in fractional passage rates have been speculated to be determined by changes in frequency of reticular contractions (Reid, 1963; Sissons et al. 1984), this speculation was not confirmed in this study. Results from chapter III showed that although the individual attributes of reticular contractions each plays a role in determining changes in both fractional passage rates and duodenal outflow of digesta, the contributory role of frequency of reticular contractions is not very significant compared to the contributory roles played by the other attributes of reticular contractions.

indeed, results frm the last study (chapter V) firmly establish that increases in fractional and duodenal outflow of digesta are not determined by changes in the frequency of reticular contractions. Similar conclusions were obtained by Ulyatt et al. (1984). Results from chapter V indicate that changes in duration, amplitude and the work done during each reticular contraction are all more important than frequency of reticular contraction in determining changes in fractional passage rates of rumen fluid and particulate matter and in duodenal outflow of digesta. Providing that the requirements of passage are adequately met, results initially obtained in the second study and confirmed in the fourth study, establish that duration as an individual attribute of reticular contraction may, be the most important determinant of passage of digesta from the RR. The importance of duration of reticular contractions in determining ruminal functions, is emphasized by results from the third study (chapter IV) which show duration as the only individual attribute of reticular contraction to have a significant positive relationship with the proportion of large feed particles appearing in the feces. These results imply that duration of reticular contractions is inextricably linked with passage rates.

There seem to be other physiological constraints which could be important in determining passage of digesta from the RR. In confirmation of results obtained by Deswysen and Ellis (1988), results from chapter V indicate some resistance to flow of neutral detergent fiber from the reticulum to the omasum, abomasum and the duodenum as determined by the difference in the extent of digestion of neutral detergent fiber at the reticulum and duodenum.

The results reported in chapter V do not clarify the equivocal nature of the relationship between time spent chewing and fractional passage and outflow rates. Similar conclusions were drawn by Macleod (1990) and Weston (1989). Although results obtained in chapter V may lend credence to the concept that the rate-limiting step in clearing feed residues from the RR may be the regulation of passage and not particle size reduction, a more definitive study in which a lower quality hay and more animals are used is required to clarify the relationship.

Passage rates of fluid and particulate matter from the RR are important determinants of voluntary intake, rumen functions such as extent of digestion of nutrients, methane production, amount of foam produced, the amount of protein which bypasses the RR, microbial growth, and overall animal productivity. Therefore effort aimed at manipulating duration of contractions may be the logical approach to achieve increases in animal productivity.

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